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Seattle, Washington

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Fishery Bulletin

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CHANGES IN BIOMASS OF FINFISHES AND SQUIDS FROM THE GULF OF MAINE TO CAPE HATTERAS, 1963-74, AS DETERMINED FROM RESEARCH VESSEL SURVEY DATA

STEPHEN H. CLARK AND BRADFORD E. BROWN[1]

ABSTRACT

Trends in finfish and squid biomass for the 1963-74 period in the International Commission for the Northwest Atlantic Fisheries (ICNAF) Subarea 5 and Statistical Area 6, as evidenced by autumn bottom trawl survey data, were reviewed. Commercial statistics reported to ICNAF reveal that landings for groundfish species of major commercial importance peaked in 1965 and subsequently declined with shifts in directed effort to major pelagic species (for which landings peaked in 1971). Trends in landings for species of lesser commercial importance primarily reflect increasing effort throughout this period.

Relative abundance indices (stratified mean catch in kilograms per tow) from the autumn bottom trawl survey revealed drastic declines in abundance of haddock, *Melanogrammus aeglefinus;* silver hake, *Merluccius bilinearis;* red hake, *Urophycis chuss;* and herring, *Clupea harengus,* during this period although decreases were observed for nearly all finfish species of commercial importance. Possible evidence of changes in species composition were also observed, in that white hake, *Urophycis tenuis;* Atlantic mackerel, *Scomber scombrus;* and squids, *Loligo pealei* and *Illex illecebrosus,* have shown pronounced increases in relative abundance in recent years coincident with declines in other species occupying similar ecological niches. Analysis for four strata sets (Middle Atlantic, southern New England, Georges Bank, and Gulf of Maine areas) reveal unadjusted declines in biomass ranging from 37% on Georges Bank to 74% in the Middle Atlantic area; by combining data for all strata, a decline of 32% was obtained for the 1967-74 period (including the Middle Atlantic section, added in 1967), while for all remaining strata (1963-74) the corresponding figure is 43%. By adjusting biomass components according to catchability and computing stock size estimates for the entire biomass, a 65% decline was obtained for all strata (including the Middle Atlantic) using untransformed abundance indices, and a 66% decline was computed from retransformed abundance indices. For the remaining strata (Middle Atlantic strata excluded) declines of 47% and 46% were obtained, respectively. By combining these data sets, the corresponding figures were 51% and 47%. Stock size estimates for 1975 approximated 2.0×10^6 tons, one-fourth of the estimated virgin biomass level and one-half of the level corresponding to maximum sustainable yield.

The continental shelf waters of the northwest Atlantic adjacent to the U.S. coast support a valuable and productive fishery resource. Prior to 1960, this area was exploited almost exclusively by a coastal fleet of U.S. vessels of under 300 gross registered tons. Landings averaged less than 500×10^3 tons[2] annually (International Commission for the Northwest Atlantic Fisheries 1953-1961), a level substantially lower than the estimated maximum sustainable yield (MSY) of approximately 950×10^3 tons obtained for this area by various investigators (Au[3]; Brown et al.[4]; Brown et al. in press). In the early 1960's, however, distant-water fleets of the U.S.S.R., Poland, and other nations entered the fishery and as that decade progressed these fleets underwent continual modernization and expansion. As a result, fishing effort and landings have increased greatly in this area in recent years. Brown et al. (in press) estimated that during the 1961-72 period standardized effort increased sixfold, while landings more than tripled. Assessments now indicate that all major stocks in this area are fully exploited and some, notably haddock, *Melanogrammus aeglefinus,* and herring, *Clupea harengus,* on Georges Bank and yellowtail flounder, *Limanda ferruginea,* off southern New England have been

[1]Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[2]Landings and estimated stock levels in this paper are given in terms of metric tons.

[3]Au, D. W. K. 1973. Total sustainable finfish yield from Subareas 5 and 6 based on yield per recruit and primary production consideration. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1973, Res. Doc. No. 10, Serial No. 2912 (mimeo.), 7 p.

[4]Brown, B. E., J. A. Brennan, E. G. Heyerdahl, M. D. Grosslein, and R. C. Hennemuth. 1973. An evaluation of the effect of fishing on the total finfish biomass in ICNAF Subarea 5 and Statistical Area 6. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1973, Res. Doc. No. 8, Serial No. 2910 (mimeo.), 30 p.

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demonstrably overfished (Hennemuth[5]; Brown and Hennemuth[6]; Schumaker and Anthony[7]). In addition, the June 1975 report of the ICNAF Standing Committee on Research and Statistics (STACRES) indicates that finfish landings for the 1971-74 period have substantially exceeded the MSY point (International Commission for the Northwest Atlantic Fisheries 1975c).

This expansion in fishing activity in recent years has stimulated considerable interest in its possible effects on biomass levels and productivity. Edwards (1968) developed biomass estimates for the area extending from Hudson Canyon to the Nova Scotia shelf (strata 1-40, Figure 1) by adjusting 1963-66 U.S. research vessel survey catches to compensate for availability and vulnerability to the survey gear by species and estimated that the annual harvest from this area (1.2×10^6 tons) approximated one-fourth of the fishable biomass during that period. He also reported a rapid decrease in fishable biomass during

[5]Hennemuth, R. C. 1969. Status of the Georges Bank haddock fishery. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1969, Res. Doc. No. 90, Serial No. 2256 (mimeo.), 21 p.

[6]Brown, B. E., and R. C. Hennemuth. 1971. Assessment of the yellowtail flounder fishery in Subarea 5. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1971, Res. Doc. No. 14, Serial No. 2599 (mimeo.), 57 p.

[7]Schumaker, A., and V. C. Anthony. 1972. Georges Bank (ICNAF Division 5Z and Subarea 6) herring assessment. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1972, Res. Doc. No. 24, Serial No. 2715 (mimeo.), 36 p.

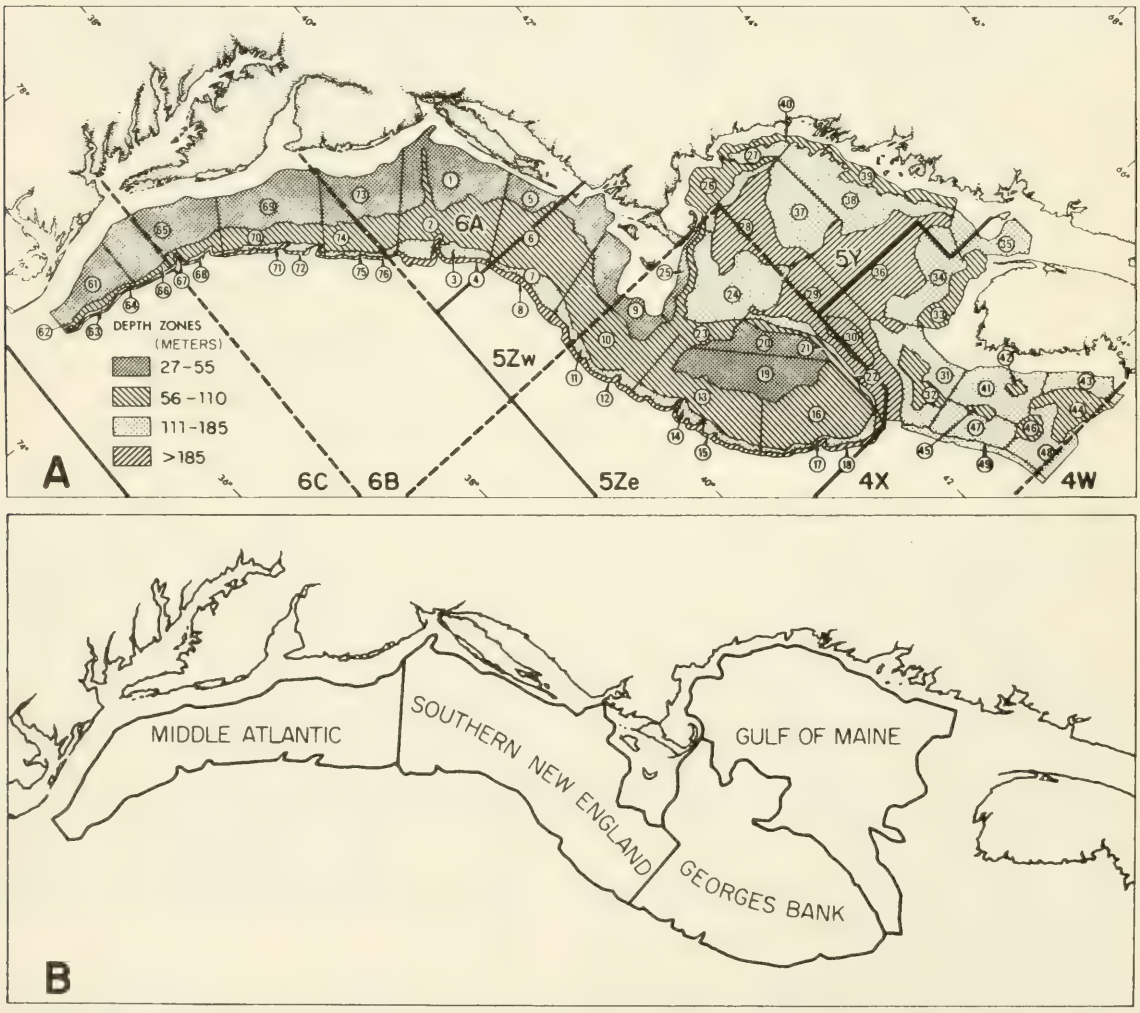

FIGURE 1.—Northwest Atlantic area from Nova Scotia to Cape Hatteras, (*a*) delineated into strata by depth, and (*b*) delineated into major units for analytical purposes, with ICNAF division boundaries superimposed.

the early and mid-1960's and noted that while the decrease had obviously been greater in the case of species for which there were directed fisheries, declines had nevertheless been general. Grosslein[8] examined autumn research vessel survey data (stratified mean catch per tow, pounds) for the 1963-71 period for southern New England and Georges Bank (strata 1-12, 13-23, and 25, Figure 1) and observed reductions in abundance of over 90% for haddock and ocean pout, *Macrozoarces americanus*, and more moderate reductions in other components of the groundfish community. Overall, Grosslein's data indicated declines in finfish biomass of 62% and 74% for southern New England and Georges Bank strata, respectively. Brown et al. (see footnote 4) presented additional analyses of Grosslein's data and documented pronounced declines for nearly all groundfish species or species groups, skates (*Raja* spp.), and sea herring; the decline for all species combined (with individual species weighted by cumulative landings for the 1962-71 period) was 64%. Brown et al. (in press) updated these analyses by including 1972 data and found an overall decline of 56%.

Since 1950, fishery management in the northwest Atlantic region has been conducted under the auspices of ICNAF, an international body currently consisting of 18 member nations pledged to cooperate in research and management of marine fishery resources in the northwest Atlantic area. This Commission, after considering the advice of various standing committees and subcommittees, formulates regulations, establishes quotas or "total allowable catches" (TAC's), and handles other matters necessary for the conservation of fish stocks in the seven regions composing the ICNAF Convention Area. The present study is concerned with the southernmost regions within this area adjoining the U.S. coast (ICNAF Subarea 5 and Statistical Area 6, Figure 1, hereafter referred to as SA 5 and 6).

In response to accumulating evidence indicating biomass declines in SA 5 and 6, STACRES in 1973 recommended an overall TAC for this area for 1974 (International Commission for the Northwest Atlantic Fisheries 1974d). Accordingly, a TAC of 923.9×10^3 tons was adopted by the Commission for 1974 to stabilize biomass levels (International Commission for the Northwest Atlantic Fisheries 1974a); for 1975, this figure was reduced to 850×10^3 tons (International Commission for the Northwest Atlantic Fisheries 1974b). In addition, STACRES further recommended that biomass levels, as measured by bottom trawl surveys, be used to monitor the effect of this regulation (International Commission for the Northwest Atlantic Fisheries 1974d).

The validity of such an approach is well documented. Grosslein (1971) has presented evidence that abundance indices derived from bottom trawl surveys are of sufficient accuracy to monitor major changes in stock size; for selected groundfish species, current levels of sampling appear adequate to detect changes on the order of 50%. Similarly, Schumaker and Anthony (see footnote 7) and Anderson[9] have found that trends in bottom trawl survey data accurately reflect major changes in stock abundance for pelagic species (herring and Atlantic mackerel, *Scomber scombrus*, respectively).

The objective of the present study was to further investigate changes in biomass of finfishes and squids in SA 5 and 6 as evidenced by trends in U.S. research vessel survey data. In this study, we have expanded on previous analyses of untransformed data (Grosslein see footnote 8; Brown et al. see footnote 4; Brown et al. in press) so as to include all available data from SA 5 and 6 for the 1963-74 period. In addition, we have attempted to compensate for anomalies in survey catch data and bias resulting from catchability differences by transforming and weighting data by species and summarizing resulting values to provide combined biomass estimates by year. We believe that the resulting trends obtained are more realistic than those derived from unadjusted survey data.

In this paper, we define biomass as consisting of weight of all species of finfishes and squids reported to ICNAF, excluding other invertebrates and large pelagic species such as swordfish, *Xiphias gladius;* sharks other than dogfish (*Squalus acanthias* and *Mustelus canis*); and tunas, *Thunnus* spp. We have also chosen to exclude inshore species such as American eel,

[8]Grosslein, M. D. 1972. A preliminary investigation of the effects of fishing on the total fish biomass, and first approximations of maximum sustainable yield for finfishes in ICNAF Division 5Z and Subarea 6. Part I. Changes in the relative biomass of groundfish in Division 5Z as indicated by research vessel surveys, and probable maximum yield of the total groundfish resource. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1972, Res. Doc. No. 119, Serial No. 2835 (mimeo.), 20 p.

[9]Anderson, E. D. 1973. Assessment of Atlantic mackerel in ICNAF Subarea 5 and Statistical Area 6. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1973, Res. Doc. No. 14, Serial No. 2916 (mimeo.), 37 p.

Anguilla rostrata; white perch, *Morone americana;* and Atlantic menhaden, *Brevoortia tyrannus*. The latter species is an important component of the biomass, but is taken primarily inshore in the southern portion of SA 6 and is, therefore, not of direct interest in the present study.

The term species, for convenience, refers to both species and species groups. Terms such as other pelagics, other fish, and groundfish refer to species so designated in ICNAF statistical bulletins (International Commission for the Northwest Atlantic Fisheries 1965-1973, 1974c, 1975a).

BOTTOM TRAWL SURVEY PROCEDURES

Autumn bottom trawl survey data have been collected by the U.S. National Marine Fisheries Service RV *ALBATROSS IV* since 1963; the RV *DELAWARE II* has also participated infrequently. In all of these surveys, both vessels have used the standard "36 Yankee" trawl with a 1.25-cm stretched mesh cod end liner. This trawl measures 10-12 m along the footrope and 2 m in height at the center of the headrope, and is equipped with rollers to make it suitable for use on rough bottom (Edwards 1968).

The area sampled extends from Nova Scotia to Cape Hatteras. A stratified random sampling design has been used in this survey (Cochran 1953); thus, the survey area has been stratified into geographical zones (Figure 1) primarily on the basis of depth (Grosslein 1969). During 1963-66, only strata from the New Jersey coast northward (1-42, Figure 1) were sampled; additional strata (61-76, Figure 1) were added in autumn 1967 to cover the mid-Atlantic region (Grosslein[10]). An additional section covering part of the Scotian Shelf was also added in 1968 but is not considered in this study.

In each cruise, sampling stations were allocated to strata roughly in proportion to the area of each stratum and were assigned to specific locations within strata at random. A 30-min tow was taken at each station at an average speed of 3.5 knots. After each tow, weight and numbers captured, fork length, and other pertinent data were recorded for each species. Data were summarized, audited, and transferred to magnetic tape following the completion of each survey. The reader is referred to Grosslein (1969, footnote 11) for further details concerning survey procedures.

Following procedures given by Cochran (1953:66) we calculated stratified mean catch per tow values in terms of weight by

$$\bar{y}_{st} = 1/N \sum_{h=1}^{k} \left[N_h \bar{y}_h \right] \quad (1)$$

where $\bar{y}_{st}$ = stratified mean catch per tow,
N_h = area of the hth stratum,
N = total area of all strata in the set,
$\bar{y}_h$ = mean catch per tow in the hth stratum, and
k = number of strata in the strata set.

We calculated the estimated population variance as

$$S^2 = 1/N \left[\sum_{h=1}^{k} \left[N_h {y_h}^2 \right] - N {y_{st}}^2 + \sum_{h-1}^{k} {s_h}^2 \left[(N_h - 1) + \frac{(N_h - N)}{N} \frac{(N_h - n_h)}{n_h} \right] \right] \quad (2)$$

where S^2 = estimated population variance,
n_h = number of tows in the hth stratum,
${s_h}^2$ = variance within the hth stratum, and
$\bar{y}_{st}$, N, N_h, $\bar{y}_h$, and k are defined as before.

We used stratified mean weight per tow (kilograms) in preference to numbers as an index of biomass change due to its convenience when working with different species groups and the high degree of variability in numbers associated with fluctuations in recruitment. Obviously, numbers would also tend to overemphasize the importance of small organisms in the community under study, as pointed out by Odum and Smalley (1959).

RECENT TRENDS IN LANDINGS

Commercial landings as reported to ICNAF (International Commission for the Northwest Atlantic Fisheries 1965-1973, 1974c, 1975a,

[10]Grosslein, M. D. 1968. Results of the joint USA-USSR groundfish studies. Part II. Groundfish survey from Cape Hatteras to Cape Cod. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1968, Res. Doc. No. 87, Serial No. 2075 (mimeo.), 28 p.

[11]Grosslein, M. D. 1969. Groundfish survey methods. NMFS, Woods Hole, Mass., Lab. Ref. No. 69-2, 34 p.

footnote 12) for the major species groups considered in this paper (principal groundfish, principal pelagics, flounders, other groundfish, other pelagics and other fish, and squid, Table 1) are given in Figures 2 and 3. Effort was concentrated on principal groundfish during the mid-1960's; landings peaked at approximately 643×10^3 tons in 1965, declined to approximately 575×10^3 tons in 1966, and dropped off sharply thereafter (Figure 2). Statistical data for individual species (International Commission for the Northwest Atlantic Fisheries 1965-73, 1974c, 1975a, see footnote 12) reveal that this pattern resulted primarily from great increases in landings of cod, haddock, and silver and red hake in the mid-1960's, followed by subsequent declines. Landings of redfish and pollock have increased somewhat in more recent years, but not enough to offset declines in the remaining species.

Landings for principal pelagics during this period (herring and mackerel) declined initially followed by a subsequent upswing. This can be attributed primarily to a diversion of USSR effort from herring to haddock and hake in 1965 and 1966 (Schumaker and Anthony see footnote 7). In 1967, however, the USSR redirected much of its effort back to the Georges Bank herring stock and also initiated an intensive mackerel fishery (Anderson see footnote 9) and other distant water fleets also began to exploit these species at about this time. This increase in effort produced increased landings of herring and mackerel to a total

[12]International Commission for the Northwest Atlantic Fisheries. 1975. Provisional nominal catches in the Northwest Atlantic, 1974 (Subareas 1 to 5 and Statistical Areas 0 and 6). Int. Comm. Northwest Atl. Fish. Annu. Meet. 1975, Summ. Doc. No. 32, Serial No. 3590 (mimeo.), 61 p.

TABLE 1.—Scientific and common names of species considered[1] in this study, grouped as in ICNAF statistical bulletins.

Common name	Scientific name
Principal groundfish (except flounders):	
Cod	*Gadus morhua*
Haddock	*Melanogrammus aeglefinus*
Redfish	*Sebastes marinus*
Silver hake	*Merluccius bilinearis*
Red hake	*Urophycis chuss*
Pollock (saithe)	*Pollachius virens*
Flounders:	
American plaice	*Hippoglossoides platessoides*
Witch	*Glyptocephalus cynoglossus*
Yellowtail	*Limanda ferruginea*
Winter flounder	*Pseudopleuronectes americanus*
Summer flounder	*Paralichthys dentatus*
Other groundfish:	
Angler	*Lophius americanus*
Cusk	*Brosme brosme*
Ocean pout	*Macrozoarces americanus*
Sculpins	*Myoxocephalus* spp.
Scup	*Stenotomus chrysops*
Searobins	*Prionotus* spp.
White hake	*Urophycis tenuis*
Principal pelagics:	
Herring	*Clupea harengus*
Mackerel	*Scomber scombrus*
Other pelagics and other fish:	
Butterfish	*Poronotus triacanthus*
Spiny dogfish	*Squalus acanthias*
Skates and rays	*Raja* spp.
Squid:	
Short-finned squid	*Illex illecebrosus*
Long-finned squid	*Loligo pealei*

[1]Note that for all groupings except principal groundfish, principal pelagics, and squid, other species were considered but are not mentioned specifically.

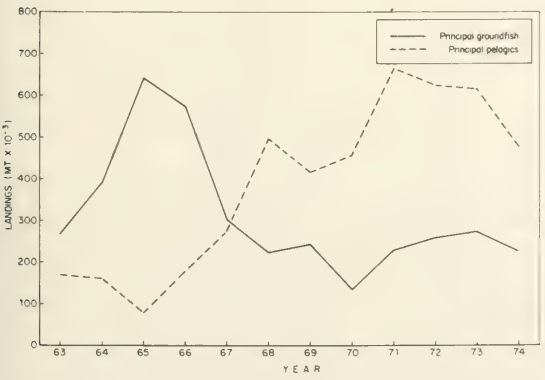

FIGURE 2.—Landings of principal groundfish and principal pelagics in ICNAF Subarea 5 and Statistical Area 6, 1963-74.

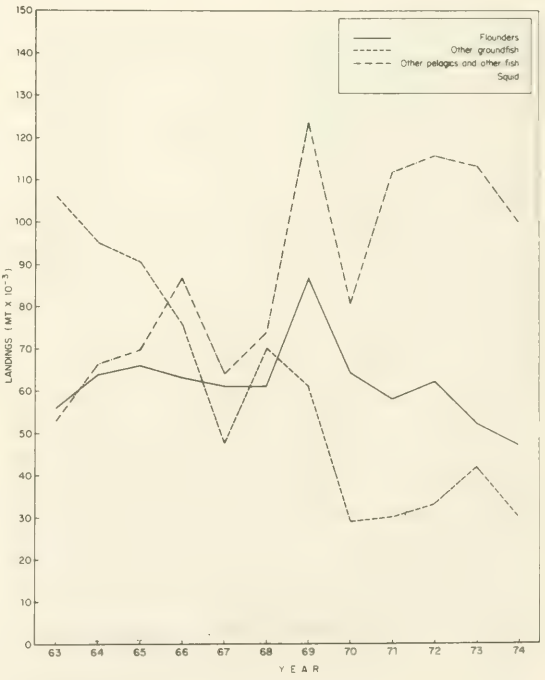

FIGURE 3.—Landings of flounders, other groundfish, other pelagics and other fish, and squid in ICNAF Subarea 5 and Statistical Area 6, 1963-74.

of approximately 667 $\times$ 10^3 tons in 1971 (Figure 2). Landings of herring and mackerel peaked in 1968 and 1972, respectively (International Commission for the Northwest Atlantic Fisheries 1965-1973, 1974c, 1975a, see footnote 12).

Landings for the remaining species groups (Figure 3) generally reflect decreasing abundance in response to increasing effort. Landings of flounders were relatively constant but did increase until 1969 followed by a gradual decline. The somewhat anomalous 1969 value resulted primarily from sharply increased catch of yellowtail by distant water fleets (Brown and Hennemuth see foonote 6). Steadily declining landings of other groundfish throughout the period of study can be attributed in part to declining abundance, while other pelagics and other fish show a general increase which would appear to be associated with increased effort as shown later. Squid landings also increased sharply since 1970.

As TAC's have been imposed for certain stocks since 1970, their possible influence should be considered. It is not believed, however, that quota management affected these trends appreciably. Species subject to quota management in 1970 and 1971 (i.e., haddock and yellowtail) had already been seriously depleted, while in 1972 and 1973 TAC's did not appear to be limiting with the exception of those imposed for haddock, yellowtail, and herring, and for the latter two species TAC's were in fact exceeded (International Commission for the Northwest Atlantic Fisheries 1975c). It appears likely that TAC's imposed for 1974 had a greater effect, particularly in the case of herring and mackerel; also, the overall TAC of 923.9 $\times$ 10^3 tons (referred to above) undoubtedly limited total catches by nation to some degree although it was exceeded by approximately 75 $\times$ 10^3 tons (International Commission for the Northwest Atlantic Fisheries 1975c). In summary, however, it would appear that the influence of quota management on the overall trends depicted in Figures 2 and 3 was relatively minor for the level of effort being exerted which, as noted previously, increased by a factor of six during the period 1962-72. It is not possible to speculate whether or not significant additional effort would have been added in 1973 and 1974 (say from new entrants to the area), had there not been regulations.

The possible influence of bias upon reported landings remains to be mentioned. In ICNAF statistical bulletins, some landings have been recorded as "not specified," e.g., "groundfish (not specified)," "other pelagics (not specified)," etc. Insofar as possible, we have combined these landings with landings data reported by species within each species group. In recent years, however, an improvement has occurred in reporting accuracy which appears to have affected the relative amounts of "not specified" landings (and thus annual totals as depicted in Figures 2 and 3). For instance, examination of data in ICNAF statistical bulletins (International Commission for the Northwest Atlantic Fisheries 1965-1973, 1974c, 1975a) reveals a decrease in the relative percentage of "not specified" groundfish of from 15 to 20% of the other groundfish category in the mid-1960's to approximately 10% in 1970-73, while for "other fish" a complete reversal of this trend occurred. The "not specified" proportion of the total "other fish" category increased from approximately 10% in the mid-1960's to 25-30% during 1970-73. This implies that landings for principal groundfish and other species may have been erroneously included under other groundfish to a greater extent in former years, thus biasing the observed trend for other groundfish downward, while the trend for other pelagics and other fish may have been biased upward due to inclusion of previously omitted landings data in more recent years. The actual extent to which trends depicted in Figures 2 and 3 were distorted by this factor is problematical, but it should be noted that for principal groundfish, principal pelagics, flounders, and squid, more important (and/or more readily identified) species were involved which probably were not affected by reporting inaccuracies to the same degree. Consequently, it is our judgement that trends for the remaining species groups were probably not appreciably biased.

CHANGES IN BIOMASS

Unweighted Analyses

Summaries of survey data by species and area permit preliminary evaluation of the magnitude and direction of change in selected biomass components in recent years and of the degree of year-to-year variability that may be encountered. Accordingly, we examined trends for different species and strata sets and for data summed over all strata before attempting transformation or weighting procedures.

Individual strata can be grouped for analysis on

the basis of stock structure, ecological factors, exploitation patterns, and availability of survey data. In the present paper, we have selected four major strata sets in SA 5 and 6 based on the above factors (Figure 1) which we considered separately prior to examination of data for the area as a whole. These are as follows:

1. Middle Atlantic area (strata 61-76, corresponding approximately to ICNAF Divisions 6B and C);
2. Southern New England area (strata 1-12, corresponding approximately to ICNAF Divisions 6A and Subdivision 5Zw);
3. Georges Bank (strata 13-25, corresponding approximately to ICNAF Subdivision 5Ze), and
4. Gulf of Maine (strata 26-30 and 36-40, corresponding approximately to ICNAF Division 5Y).

The rationale for this arrangement is based on differences in faunal assemblages although exploitation patterns and data availability were also considered. A number of stock identification studies support such an arrangement (Wise 1962; Grosslein 1962; Anthony and Boyar 1968; Ridgway et al.[13]; Anderson[14]; and others). In addition, Grosslein's[15] study indicated a relatively high diversity of species in the southern New England-Middle Atlantic areas in contrast to the Gulf of Maine, with Georges Bank being a rather transitional area. Exploitation patterns and reporting of commercial fishery statistics also dictate some form of division between Subdivision 5Ze and the Subdivision 5Zw-Statistical Area 6 region and other areas to the north or south (Figure 1). Finally, the fact that survey data are nonexistent for Middle Atlantic strata prior to 1967 required a division between this area and the remainder of SA 5 and 6 for analytical purposes.

Trends in relative abundance from 1963 to 1974 (stratified mean catch per tow [kilograms], U.S. autumn bottom trawl survey data) are given by area for selected species in Tables 2-5 and for major ICNAF categories in Figures 4-9. Pronounced declines of principal groundfish are evident both on Georges Bank and in the Gulf of Maine, with lesser declines in the remaining areas (Figure 4). The trends observed resulted primarily from declining relative abundance of haddock and silver and red hake (Tables 2-5). Haddock, in particular, appears to have greatly decreased on

[13]Ridgway, G. J., R. D. Lewis, and S. Sherburne. 1969. Serological and biochemical studies of herring populations in the Gulf of Maine. Cons. Perm. Int. Explor. Mer, Memo No. 24, 6 p.

[14]Anderson, E. D. 1974. Comments on the delineation of red and silver hake stocks in ICNAF Subarea 5 and Statistical Area 6. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1974, Res. Doc. No. 100, Serial No. 3336 (mimeo.), 8 p.

[15]Grosslein, M. D. 1973. Mixture of species in Subareas 5 and 6. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1973, Res. Doc. No. 9, Serial No. 2911 (mimeo.), 20 p.

TABLE 2.—Stratified mean catch per tow (kilograms) for selected species of finfish and squid, *Albatross IV* autumn bottom trawl survey data, 1967-74, Middle Atlantic area (strata 61-76).

Species	1967	1968	1969	1970	1971	1972	1973	1974
Principal groundfish:								
Silver hake	0.9	0.9	0.1	0.2	0.3	0.5	0.4	[1]0.0
Red hake	0.1	0.8	0.5	0.2	0.4	0.2	0.1	0.0
Flounders:								
Yellowtail	3.4	5.5	3.6	[1]0.0	0.3	0.1	[1]0.0	0.0
Winter flounder	1.7	1.3	0.6	[1]0.0	0.2	0.1	0.1	0.0
Summer flounder	2.0	1.5	0.8	[1]0.0	0.4	0.1	0.3	0.8
Other	0.7	2.0	0.6	0.4	0.8	1.0	1.6	0.5
Other groundfish:								
Angler	0.7	0.6	0.3	[1]0.0	0.1	1.4	0.9	[1]0.0
Scup	2.6	0.8	8.4	0.1	0.3	3.2	0.2	0.7
Searobins	130.1	13.8	5.4	6.9	3.1	1.7	1.9	1.9
Other	0.5	0.3	0.3	[1]0.0	[1]0.0	[1]0.0	[1]0.0	0.0
Principal pelagics:								
Herring	0.0	0.0	0.0	0.0	0.0	0.0	[1]0.0	0.0
Mackerel	[1]0.0	0.1	0.0	0.0	[1]0.0	0.0	0.0	0.0
Other pelagics and other fish:								
Butterfish	3.6	18.1	3.9	5.4	5.0	4.2	11.0	3.7
Spiny dogfish	47.8	3.1	4.9	0.0	0.0	0.0	[1]0.0	0.0
Skates and rays	4.0	8.4	29.5	7.0	12.8	6.6	10.4	5.4
Other[2]	9.8	7.0	4.5	5.9	9.6	3.1	9.4	3.3
Squid:								
Short-finned squid	0.3	0.2	0.1	0.4	0.2	0.3	[1]0.0	0.1
Long-finned squid	10.6	9.3	9.2	4.8	2.5	12.6	11.2	11.1
Total finfish and squid	218.8	73.7	72.7	31.3	36.0	35.1	47.5	27.5

[1]Less than 0.05.
[2]Does not include data for tunas, sharks, swordfish, American eel, or white perch.

TABLE 3.—Stratified mean catch per tow (kilograms) for selected species of finfish and squid, *Albatross IV* autumn bottom trawl survey data, 1963-74, southern New England area (strata 1-12).

Species	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
Principal groundfish:												
Cod	3.0	0.5	1.8	0.7	2.9	0.8	1.5	0.6	0.1	2.1	[1]0.0	0.4
Haddock	2.7	7.1	1.2	0.1	0.5	[1]0.0	0.1	0.5	0.1	0.0	[1]0.0	0.0
Silver hake	5.2	5.7	7.6	3.6	4.4	4.8	2.3	2.6	4.6	4.0	3.2	1.3
Red hake	8.1	4.4	5.6	2.9	2.7	4.4	4.8	3.9	3.4	6.6	3.0	0.5
Flounders:												
Yellowtail	12.0	11.8	8.7	7.9	11.9	11.1	12.3	13.7	7.6	26.8	2.6	1.2
Winter flounder	2.4	3.1	3.1	2.1	1.5	1.0	1.3	2.4	1.0	3.0	0.5	0.4
Other	4.8	3.8	2.7	4.5	1.9	2.9	1.7	1.9	1.3	2.9	2.4	2.9
Other groundfish:												
Angler	4.4	7.0	4.9	6.7	1.9	1.2	2.5	2.8	1.5	9.8	2.9	1.0
Ocean pout	0.7	0.4	0.3	1.1	0.6	0.5	0.3	0.3	0.1	0.1	0.2	0.0
Sculpins	0.3	1.0	1.7	2.5	1.6	1.0	1.4	1.1	0.3	2.2	0.1	0.1
Scup	1.3	2.5	0.7	0.5	0.6	0.4	1.6	0.4	0.2	1.9	1.6	1.4
Searobins	1.0	0.8	0.5	0.7	0.8	0.3	0.5	0.2	0.3	4.7	0.3	0.1
White hake	1.2	0.4	0.6	1.2	1.3	1.4	0.6	0.5	0.4	0.4	0.1	0.1
Other	0.1	0.1	0.1	[1]0.0	0.3	[1]0.0	0.1	0.1	0.3	[1]0.0	[1]0.0	0.0
Principal pelagics:												
Herring	0.2	[1]0.0	0.5	1.8	0.5	0.1	[1]0.0	[1]0.0	[1]0.0	[1]0.0	0.0	0.0
Mackerel	[1]0.0	[1]0.0	[1]0.0	[1]0.0	1.0	0.2	3.9	[1]0.0	0.1	[1]0.0	[1]0.0	[1]0.0
Other pelagics and other fish:												
Butterfish	2.6	6.0	4.5	1.5	2.2	4.0	6.5	1.1	5.8	2.4	6.3	6.1
Spiny dogfish	71.2	194.4	93.0	92.4	96.9	58.5	216.5	67.6	13.2	32.7	46.1	18.6
Skates and rays	15.8	10.4	11.3	13.6	3.7	1.2	2.3	2.9	6.6	9.1	3.0	3.2
Other[2]	0.1	1.9	2.0	0.7	1.7	1.3	4.1	5.1	4.1	3.1	5.3	5.2
Squid:												
Short-finned squid	([3])	[4]0.1	[4]0.1	[4]0.1	0.5	0.7	0.1	0.3	0.3	0.6	0.1	0.2
Long-finned squid	([3])	[4]1.2	[4]1.6	[4]2.2	2.0	12.2	18.1	3.6	5.4	6.7	16.7	12.1
Total finfish and squid	137.1	262.6	152.5	146.8	141.4	108.0	282.5	111.6	56.7	119.1	94.4	54.8

[1]Less than 0.05
[2]Does not include data for tunas, sharks, swordfish, American eel, or white perch
[3]Data not recorded
[4]Squid catches for 1964-66 prorated by species according to relative percentages caught in later years

TABLE 4.—Stratified mean catch per tow (kilograms) for selected species of finfish and squid, *Albatross IV* autumn bottom trawl survey data, 1963-74, Georges Bank area (strata 13-25).

Species	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
Principal groundfish:												
Cod	11.0	7.1	7.2	5.0	8.4	5.3	4.9	7.8	6.1	14.2	19.1	5.1
Haddock	51.2	75.2	56.1	21.4	20.5	9.3	5.8	10.6	3.6	5.1	7.2	2.8
Redfish	0.9	4.0	1.1	2.0	2.6	3.5	6.5	4.6	1.9	3.9	2.6	1.9
Silver hake	5.4	1.7	1.6	2.1	1.0	2.2	1.6	2.3	1.2	2.4	2.4	1.5
Red hake	7.4	2.2	1.8	1.2	0.8	1.1	1.5	0.9	1.9	1.2	2.8	1.4
Pollock	2.3	2.1	1.7	2.9	1.1	1.0	1.4	0.4	2.2	1.0	1.6	0.4
Flounders:												
American plaice	5.5	2.0	1.2	3.3	1.7	1.3	1.1	1.5	0.9	0.9	0.9	0.4
Witch	1.0	0.5	0.5	1.5	0.6	0.9	0.5	1.5	0.5	1.0	1.5	0.4
Yellowtail	8.2	8.4	5.6	2.5	4.5	6.7	5.4	3.0	3.7	4.0	3.8	2.2
Winter flounder	1.8	2.1	2.0	3.6	1.3	1.5	1.7	4.7	1.0	1.5	1.6	1.5
Other	1.0	0.7	0.6	1.1	1.1	1.2	1.3	0.4	0.6	1.3	3.5	1.8
Other groundfish:												
Angler	3.5	2.6	5.0	5.8	0.5	1.9	1.1	0.7	0.6	1.6	2.2	1.1
Ocean pout	1.7	1.0	0.9	0.9	0.2	0.1	[1]0.0	0.1	[1]0.0	0.4	0.2	[1]0.0
Sculpins	3.4	1.8	3.3	3.3	2.0	3.8	3.1	4.9	3.1	2.8	3.6	2.0
White hake	1.4	0.5	0.8	[1]0.0	1.6	1.0	1.8	2.4	2.2	2.2	3.5	2.0
Other	0.5	0.5	0.6	1.0	0.7	1.0	0.2	0.5	0.1	0.4	0.7	0.3
Principal pelagics:												
Herring	1.0	0.2	0.9	1.5	0.6	0.2	0.2	[1]0.0	0.3	0.1	[1]0.0	[1]0.0
Mackerel	[1]0.0	0.0	0.1	0.1	0.2	0.2	0.4	0.1	[1]0.0	0.4	[1]0.0	0.3
Other pelagics and other fish:												
Butterfish	0.7	1.3	0.3	0.1	0.6	1.0	0.3	0.2	1.1	1.2	0.4	1.0
Spiny dogfish	2.9	3.0	3.5	1.8	2.5	5.6	2.4	3.5	3.3	9.7	36.2	2.2
Skates and rays	31.3	15.0	21.7	17.7	15.2	12.3	8.7	15.7	8.9	15.4	28.9	15.4
Other[2]	0.5	0.4	0.5	0.5	0.5	0.4	0.4	0.2	0.6	0.9	1.0	2.8
Squid:												
Short-finned squid	([3])	[4]0.2	[4]0.5	[4]0.3	0.1	0.3	[1]0.0	0.2	0.4	0.2	5.0	0.1
Long-finned squid	([3])	[4]0.2	[4]0.5	[4]0.4	0.4	0.4	1.5	1.1	1.0	1.1	0.1	2.2
Total finfish and squid	142.6	132.7	118.0	80.0	68.7	62.2	51.8	67.3	45.2	72.9	128.8	48.8

[1]Less than 0.05.
[2]Does not include data for tunas, sharks, swordfish, American eel, or white perch.
[3]Data not recorded.
[4]Squid catches for 1964-66 prorated by species according to relative percentages caught in later years.

TABLE 5.—Stratified mean catch per tow (kilograms) for selected species of finfish and squid, *Albatross IV* autumn bottom trawl survey data, 1963-74, Gulf of Maine area (strata 26-30 and 36-40).

Species	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
Principal groundfish:												
Cod	10.9	14.1	7.4	8.0	5.7	12.0	9.5	10.2	10.2	8.0	5.4	5.5
Haddock	39.1	14.2	12.8	10.1	9.8	11.9	7.8	4.3	5.1	3.2	5.3	2.2
Redfish	26.9	59.1	14.0	31.8	25.7	43.2	21.3	33.8	25.4	25.0	17.3	26.4
Silver hake	28.3	4.8	8.7	4.2	2.6	2.0	2.6	2.4	3.0	6.3	4.0	3.9
Red hake	4.9	0.7	1.0	0.8	0.3	0.1	0.3	0.1	1.0	2.0	0.5	0.5
Pollock	8.6	7.8	3.6	2.4	2.9	5.4	13.1	3.6	5.5	8.4	5.9	6.2
Flounders:												
American plaice	6.2	3.6	6.0	6.3	3.5	4.3	3.5	2.5	2.9	2.2	2.9	2.3
Witch	3.6	2.3	2.5	4.5	2.0	3.7	5.1	3.4	3.2	2.3	1.3	1.6
Other	1.1	0.4	1.0	0.1	[1]0.0	0.1	1.2	0.3	0.1	0.7	0.2	0.6
Other groundfish:												
Angler	3.7	1.6	1.9	3.6	1.7	2.0	4.5	3.1	4.0	1.5	3.6	2.3
Cusk	2.2	1.2	1.3	3.8	1.1	1.8	1.7	2.0	1.8	3.0	1.3	0.5
White hake	7.8	5.2	7.9	9.5	4.2	5.8	17.7	16.3	15.3	16.9	15.9	14.0
Other	0.3	0.4	0.6	1.0	0.2	0.5	0.1	0.6	0.3	0.8	0.4	0.3
Principal pelagics:												
Herring	1.6	0.1	0.2	0.3	0.1	[1]0.0	[1]0.0	0.1	0.6	[1]0.0	[1]0.0	[1]0.0
Mackerel	[1]0.0	0.0	0.0	[1]0.0	0.0	[1]0.0	[1]0.0	[1]0.0	[1]0.0	[1]0.0	[1]0.0	[1]0.0
Other pelagics and other fish:												
Spiny dogfish	58.2	10.6	11.8	4.0	7.8	22.8	9.8	18.3	11.9	17.3	7.2	8.7
Skates and rays	15.1	9.4	11.1	17.4	4.9	10.0	14.4	16.2	12.1	7.9	7.6	4.4
Other[2]	2.5	0.1	0.2	0.3	0.4	0.2	0.1	0.3	0.2	0.3	0.2	0.2
Squid:												
Short-finned squid	([3])	[1,4]0.0	[4]0.2	[4]0.4	0.1	0.1	0.1	0.3	0.5	0.2	0.6	1.2
Long-finned squid	([3])	[4]0.0	[1,4]0.0	[4]0.1	[1]0.0	[1]0.0	[1]0.0	[1]0.0	[1]0.0	[1]0.0	[1]0.0	[1]0.0
Total finfish and squid	221.0	135.6	92.2	108.6	73.0	125.9	112.8	117.8	103.2	106.0	79.6	80.8

[1]Less than 0.05.
[2]Does not include data for tunas, sharks, swordfish, American eel, or white perch.
[3]Data not recorded.
[4]Squid catches for 1964-66 prorated by species according to relative percentages caught in later years.

FIGURE 4.—Catch of principal groundfish in U.S. autumn bottom trawl surveys for the Middle Atlantic (strata 61-76), 1967-74, and for southern New England (strata 1-12), Georges Bank (strata 13-25), and the Gulf of Maine (strata 26-30 and 36-40), 1963-74.

Georges Bank and in the Gulf of Maine and to be almost nonexistent in southern New England waters. Relative abundance indices for redfish and pollock, however, appear to have remained relatively stable (Tables 4, 5). Cod declined somewhat in the Gulf of Maine but remained relatively stable in other areas (Tables 3-5).

Catches of flounders indicate substantial declines in relative abundance for all areas (Figure 5) and nearly all species (Tables 2-5) with yellowtail declining very sharply in recent years. Unusually high catches of yellowtail were taken in southern New England waters in 1972 (Figure 5, Table 3); factors involved are unclear but appear to reflect changes in availability, as actual increases in abundance do not appear to have occurred (Parrack[16]).

Data for other groundfish (Figure 6) suggest a decline in biomass for Middle Atlantic strata, an increase for Gulf of Maine strata, and relatively stable levels elsewhere. The observed trend for Middle Atlantic strata is strongly influenced by large catches of searobins in 1967 (Table 2) which

[16]Parrack, M. L. 1973. Current status of the yellowtail flounder fishery in ICNAF Subarea 5. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1973, Res. Doc. No. 104, Serial No. 3067 (mimeo.), 5 p.

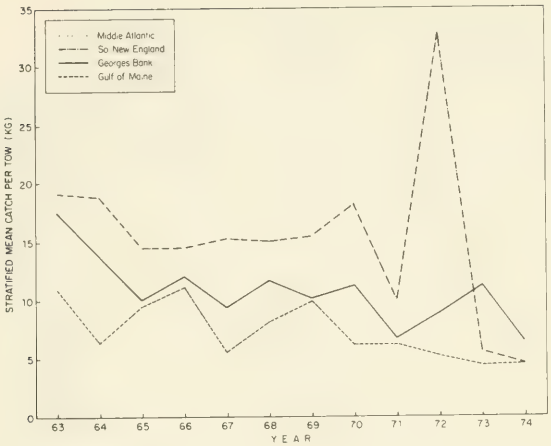

FIGURE 5.—Catch of flounders in U.S. autumn bottom trawl surveys for the Middle Atlantic (strata 61-76), 1967-74, and for southern New England (strata 1-12), Georges Bank (strata 13-25), and the Gulf of Maine (strata 26-30 and 36-40), 1963-74.

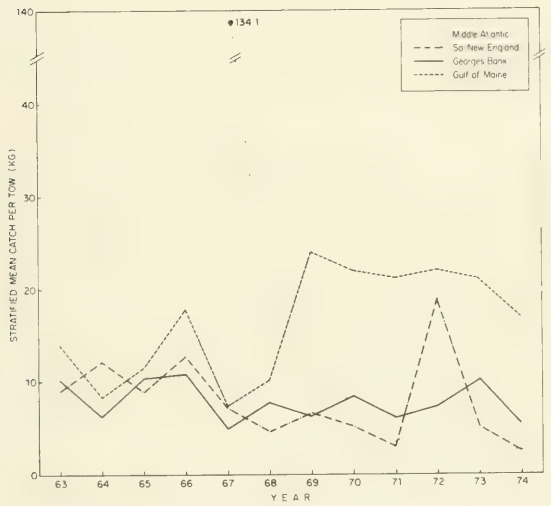

FIGURE 6.—Catch of other groundfish in U.S. autumn bottom trawl surveys for the Middle Atlantic (strata 61-76), 1967-74, and for southern New England (strata 1-12), Georges Bank (strata 13-25), and the Gulf of Maine (strata 26-30 and 36-40), 1963-74.

continued to decline in succeeding years. Ocean pout also appear to have declined sharply during the period of study in southern New England and Georges Bank strata (Tables 3, 4). Abundance of white hake, however, appears to have increased in the Gulf of Maine in recent years (Table 5), leading to an increase in other groundfish biomass for these strata.

Principal pelagics appear to have declined in relative abundance although considerable fluctuation is evident (Figure 7). Most of this variation is, however, associated with the presence of outstanding year-classes of herring in the early and mid-1960's (Schumaker and Anthony see footnote 7) and the appearance of an outstanding year-class of mackerel in 1967 (Anderson see footnote 9). Considerable fluctuation is also evident in catches of other pelagics and other fish (Figure 8, Tables 2-5) although the trend is generally downward (anomalous peaks relate primarily to high catches of spiny dogfish in certain years). Data for squid (Figure 9) indicate increased abundance although catches of long-finned squid appear to be lower in 1970 and 1971 in Middle Atlantic strata and from 1970 to 1972 in southern New England strata than in the years immediately preceding and following (Tables 2, 3). The actual degree of change throughout the period of study is uncertain, however, in that complete records of catches for squid were not kept prior to 1967.

A summary of trends in relative abundance by area is given in Tables 6 and 7 and Figure 10. We computed percentage changes from mean catch values (averaged over 1967-68 and 1973-74 for Middle Atlantic strata and 1963-65 and 1972-74 for all other strata sets). We obtained declines of

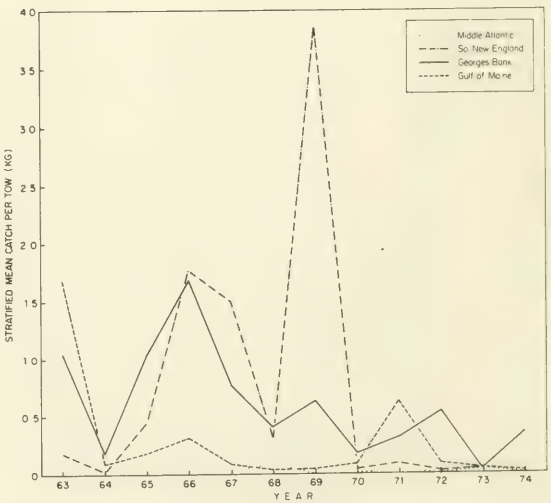

FIGURE 7.—Catch of principal pelagic species in U.S. autumn bottom trawl surveys for the Middle Atlantic (strata 61-76), 1967-74, and for southern New England (strata 1-12), Georges Bank (strata 13-25), and the Gulf of Maine (strata 26-30 and 36-40), 1963-74.

FIGURE 8.—Catch of other pelagics and other fish in U.S. autumn bottom trawl surveys for the Middle Atlantic (strata 61-76), 1967-74, and for southern New England (strata 1-12), Georges Bank (strata 13-25), and the Gulf of Maine (strata 26-30 and 36-40), 1963-74.

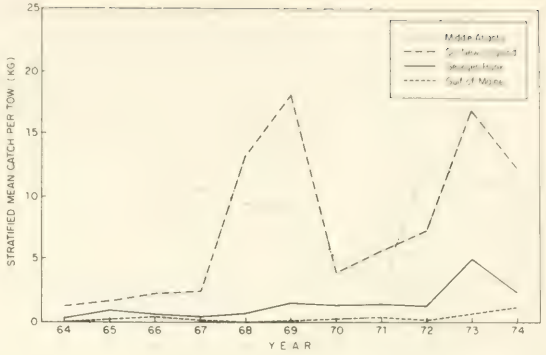

FIGURE 9.—Catch of squid in U.S. autumn bottom trawl surveys for the Middle Atlantic (strata 61-76), 1967-74, and for southern New England (strata 1-12), Georges Bank (strata 13-25), and the Gulf of Maine (strata 26-30 and 36-40), 1963-74.

FIGURE 10.—Catch of total finfish and squid in U.S. autumn bottom trawl surveys for the Middle Atlantic (strata 61-76), 1967-74, and for southern New England (strata 1-12), Georges Bank (strata 13-25), and the Gulf of Maine (strata 26-30 and 36-40), 1963-74.

over 90% for certain species, while for all data combined we obtained declines of 74%, 52%, 37%, and 41% for the Middle Atlantic, southern New England, Georges Bank, and Gulf of Maine areas, respectively. Omission of catches of searobins for the Middle Atlantic area, however, reduces that value to 52%. Further omitting data for squid for all strata sets (as squid catches were inadequately recorded during the early years of the survey) provides corresponding declines of 62%, 58%, 38%, and 41%. Consequently, even greater declines may be more realistic than those initially computed.

After examining data for the above strata sets, we evaluated trends for the entire region by combining data over all strata (Tables 8, 9) and compared between means of initial and final periods (1967-68/1973-74 data for all strata; 1963-65/1972-74 data, Middle Atlantic strata excluded). For 1967-74, all strata (Table 8), we observed a decline of 32%, while for 1963-74, Middle Atlantic strata excluded (Table 9), the decline is 43%. The corresponding figures are 37% and 46%, respectively, with squid omitted.

The above data demonstrate that significant changes in biomass levels occurred in SA 5 and 6 after the early 1960's. It will be noted, however, that the summaries presented above are biased by "catchability" differences among species and do

TABLE 6.—Stratified mean catch per tow (kilograms) for selected species, *Albatross IV* fall survey data, Middle Atlantic (1967-68 and 1973-74) and southern New England (1963-65 and 1972-74) areas.[1] Mean catch per tow values represent simple averages of values given in Tables 2 and 3 for these areas and years.

	Middle Atlantic			Southern New England		
Species	1967-68 mean	1973-74 mean	% change	1963-65 mean	1972-74 mean	% change
Principal groundfish:						
Cod	0.0	0.0	0	1.7	0.8	−53
Haddock	0.0	0.0	0	3.7	[2]0.0	−99
Silver hake	0.9	0.2	−78	6.2	2.8	−55
Red hake	0.5	0.1	−80	6.0	3.4	−43
Flounders:						
Yellowtail	4.5	[2]0.0	−99	10.8	10.2	− 6
Summer flounder	1.8	0.5	−72	0.5	0.9	+80
Winter flounder	1.5	0.1	−93	2.9	1.3	−55
Other	1.2	1.1	−8	3.3	1.8	−45
Other groundfish:						
Angler	0.7	0.5	−29	5.4	4.5	−17
Ocean pout	[2]0.0	[2]0.0	− 0	0.5	0.1	−80
Sculpins	0.1	0.0	−100	1.0	0.8	−20
Scup	1.7	0.5	−71	1.5	1.6	+7
Searobins	71.9	1.9	−97	0.7	1.7	+143
White hake	0.1	0.0	−100	0.8	0.2	−75
Other	0.3	[2]0.0	−99	0.1	[2]0.0	−99
Principal pelagics:						
Herring	0.0	[2]0.0	+0	0.2	[2]0.0	−99
Mackerel	0.1	0.0	−100	[2]0.0	[2]0.0	+0
Other pelagics and other fish:						
Butterfish	10.9	7.4	−32	4.4	4.9	+11
Spiny dogfish	25.5	[2]0.0	−100	119.4	32.5	−73
Skates and rays	6.2	7.9	+27	12.5	5.1	−59
Other	8.4	6.4	−24	1.3	4.5	+246
Squid:						
Short-finned squid	0.3	0.1	−67	0.1	0.3	+200
Long-finned squid	9.9	11.1	+12	1.4	11.8	+743
Total finfish and squid	146.5	37.8	−74	184.4	89.2	−52

[1]Middle Atlantic and southern New England areas represented by strata sets 61-76 and 1-12, respectively.
[2]Less than 0.05.

TABLE 7.—Stratified mean catch per tow (kilograms) for selected species, *Albatross IV* fall survey data, Georges Bank and Gulf of Maine areas,[1] 1963-65 and 1972-74. Mean catch per tow values represent simple averages of values given in Tables 4 and 5 for these areas and years.

	Georges Bank			Gulf of Maine		
Species	1963-65 mean	1972-74 mean	% change	1963-65 mean	1972-74 mean	% change
Principal groundfish:						
Cod	8.4	12.8	+52	10.8	6.3	−42
Haddock	60.8	5.0	−92	22.0	3.5	−84
Redfish	2.0	2.8	+40	33.3	22.9	−31
Silver hake	2.9	2.1	−28	13.9	4.7	−66
Red hake	3.8	1.8	−53	2.2	1.0	−55
Pollock	2.0	1.0	−50	6.7	6.8	+1
Flounders:						
American plaice	2.9	0.7	−76	5.3	2.4	−55
Yellowtail	7.4	3.4	−54	0.4	0.2	−50
Winter flounder	2.0	1.5	−25	0.4	0.3	−25
Witch	0.7	1.0	+43	2.8	1.7	−39
Other	0.8	2.2	+175	0.1	[2]0.0	−99
Other groundfish:						
Angler	3.7	1.6	−57	2.4	2.5	+4
Cusk	0.3	0.2	−33	1.6	1.6	0
Ocean pout	1.2	0.2	−83	[2]0.0	0.1	+474
Sculpins	2.8	2.7	−4	0.2	0.2	0
White hake	0.9	2.6	+189	6.9	15.6	+126
Other	0.2	0.3	+50	0.3	0.1	−66
Principal pelagics:						
Herring	0.7	[2]0.0	−99	0.6	[2]0.0	−99
Mackerel	[2]0.0	0.2	+300	[2]0.0	[2]0.0	0
Other pelagics and other fish:						
Spiny dogfish	3.1	16.0	+416	26.9	11.1	−59
Skates and rays	22.7	19.9	−12	11.9	6.6	−45
Other	1.2	2.4	+100	0.8	0.2	−75
Squid:						
Short-finned squid	0.4	1.8	+350	0.1	0.7	+600
Long-finned squid	0.4	1.1	+175	[2]0.0	[2]0.0	0
Total finfish and squid	131.3	83.3	−37	149.6	88.5	−41

[1]Georges Bank and Gulf of Maine areas represented by strata sets 13-25 and 26-30 and 36-40, respectively.
[2]Less than 0.05.

TABLE 8.—Stratified mean catch per tow (kilograms) for selected species of finfish and squid, *Albatross IV* autumn bottom trawl survey data, 1967-74, Middle Atlantic, southern New England, Georges Bank, and Gulf of Maine (strata 61-76, 1-30, and 36-40).

Species	1967	1968	1969	1970	1971	1972	1973	1974
Cod	4.5	5.0	4.4	5.1	4.6	6.4	6.4	2.9
Haddock	8.1	5.8	3.8	4.0	2.4	2.2	3.3	1.3
Redfish	8.2	13.6	7.9	11.1	7.9	8.3	5.7	7.7
Silver hake	2.3	2.5	1.8	2.0	2.4	3.6	2.6	1.9
Red hake	1.0	1.6	1.8	1.3	1.7	2.6	1.6	0.7
Pollock	1.2	1.9	4.2	1.2	2.2	2.7	2.1	1 8
Yellowtail	4.8	5.6	5.2	4.2	2.9	7.9	1 6	1.0
Other flounder	4.6	5.4	5.1	5.1	3.5	4.3	4.2	3.5
Herring	0.3	0.1	0.1	[1]0.0	0.3	0.1	[1]0.0	[1]0.0
Mackerel	0.3	0.2	1.1	[1]0.0	[1]0.0	0.1	[1]0.0	[1]0.0
Other finfish[2]	80.9	47.1	89.2	49.3	33.6	43.3	54.5	27.4
Short-finned squid	0.2	0.3	0.1	0.3	0.4	0.3	0.3	0.4
Long-finned squid	2.8	5.1	6.8	2.2	2.1	4.6	7.6	5.8
Total finfish and squid	119.2	94.2	131.5	85.8	64.0	86.4	89.9	54.4

[1]Less than 0.05.
[2]Does not include data for tunas, sharks, swordfish, American eel, or white perch.

TABLE 9.—Stratified mean catch per tow (kilograms) for selected species of finfish and squid, *Albatross IV* autumn bottom trawl survey data, 1963-74, southern New England, Georges Bank, and Gulf of Maine areas (strata 1-30 and 36-40).

Species	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
Cod	8.5	7.6	5.6	4.8	5.7	6.4	5.6	6.4	5.7	8.1	8.0	3.6
Haddock	31.6	31.2	22.9	10.5	10.2	7.4	4.7	5.1	3.1	2.8	4.2	1.6
Redfish	10.3	23.1	5.8	12.4	10.4	17.1	10.0	14.0	10.0	10.5	7.2	10 0
Silver hake	13.8	4.1	6.1	3.3	2.7	2.9	2.2	2.4	2.9	4.4	3.2	2.4
Red hake	6.7	2.3	2.7	1.6	1.2	1.8	2.1	1.6	2.0	3.2	2.0	0.8
Pollock	4.1	3.6	1.9	1.8	1.5	2.3	5.3	1.5	2.7	3.4	2.7	2.2
Yellowtail	6.6	6.5	4.5	3.2	5.2	5.6	5.6	5.3	3.6	9.8	2.1	1 2
Other flounder	8.8	6.1	6.7	9.2	4.6	5.6	5.8	6.3	4.0	5.1	4.8	4.0
Herring	1.0	0.1	0.5	1.2	0.4	0.1	0.1	0.1	0.3	0.1	[1]0.0	0.1
Mackerel	[1]0.0	[1]0.0	0.1	0.1	0.4	0.2	1.4	0.1	0.1	0.2	0.1	0.1
Other finfish[2]	75.6	89.4	61.8	62.9	49.8	45.8	97.5	55.5	33.7	49.4	59.9	30.6
Short-finned squid	([3])	[1,4]0.0	[4]0.1	[4]0.1	0.2	0.4	0.1	0.3	0.4	0.3	0.4	0.5
Long-finned squid	([3])	[4]0.5	[4]0.8	[4]1.0	0.8	4.0	6.2	1.5	2.0	2.5	6.7	4.5
Total finfish and squid	167.0	174.5	119.5	112.1	93.1	99.6	146.6	100.1	70.5	99.8	101.3	61.6

[1]Less than 0.05.
[2]Does not include data for tunas, sharks, swordfish, American eel, or white perch
[3]Data not recorded.
[4]Squid catches for 1964-66 prorated by species according to relative percentages caught in later years.

not reflect the relative magnitude of various species within the biomass as a whole. For instance, herring and mackerel together appear to have constituted over 50% of the biomass present during this study (Edwards 1968; International Commission for the Northwest Atlantic Fisheries 1974e, footnote 17) yet account for less than 1% of the weight taken in autumn bottom trawl surveys. Furthermore, the aggregated distribution of finfishes and squid in nature, and the behavior of the gear employed, insure that catch data for individual species will seldom be normally distributed but rather will tend to conform to the negative binomial or some other contagious form (Taylor 1953). In the following sections, we utilize selected transformation and weighting procedures in attempts to correct for these factors.

Weighted Analyses

Catchability differences among species imply that trends in biomass as defined in this study will be primarily determined by trends for species most vulnerable to the survey gear unless adjustments in terms of catchability are made. Accordingly, we developed catchability coefficients by year for the species and species groups in Tables 8 and 9 for use in computing weighting factors by relating stratified mean catch per tow by stock to available estimates of stock size, all computations being in terms of weight. Annual estimates of stock size (weight at the beginning of year i) were required for this purpose for each individual stock for which TAC's have been established (International Commission for the Northwest Atlantic Fisheries 1975c); thus, separate estimates were required for cod in 5Y[18] and 5Z, haddock in 5Ze, silver hake in

[17]International Commission for the Northwest Atlantic Fisheries. 1975. Report of the herring working group, April 1975. ICNAF Annu. Meet. 1975, Summ Doc. No. 19, Serial No. 3499 (mimeo.), 31 p.

[18]Alphanumeric designations refer to divisions and subdivisions of SA 5 and 6 given in Figure 1.

5Y, 5Ze, and 5Zw-SA 6, red hake in 5Ze and 5Zw-SA 6, yellowtail in 5Ze, 5Zw, and SA 6, and herring in 5Y and 5Z-SA 6. (We considered the remaining species and species groups indicated as stocks for the purpose of this analysis.) Silver hake, herring, and mackerel stock sizes were available from virtual population analyses in previous assessments (International Commission for the Northwest Atlantic Fisheries 1974e, see footnote 17; Anderson[19,20]), while annual estimates for haddock and red hake had also been computed earlier (Hennemuth see footnote 5; Anderson[21]; Clark[22]) using average weight or mean weight at age data and the relationship:

$$C_i = N_i F_i / Z_i (1 - \exp[-Z_i]) \quad (3)$$

where C_i = landings (number) in year i,
N_i = stock size (number) at the beginning of year i,
F_i = instantaneous fishing mortality rate in year i, and
Z_i = instantaneous total mortality rate in year i ($=F_i + M$, the instantaneous natural mortality rate).

Approximations of stock size for both long-finned and short-finned squids are also available for recent years (International Commission for the Northwest Atlantic Fisheries 1975c). We used these approximations for all years in view of uncertainty regarding stock size and historical trends in abundance for these species (International Commission for the Northwest Atlantic Fisheries 1975c).

Stock size estimates for the remaining species and species groups are currently unavailable, and we computed estimates by a variety of procedures. For yellowtail, we assumed an F value of 1.0 for the southern New England (5Zw) stock in 1967-68 ($M = 0.2$ in all cases) based on earlier assessment work (Brown and Hennemuth see footnote 6), and calculated stock size for each year using Equation (3); 1964-66 stock sizes were then assumed to be similar to the 1967-68 average as commercial abundance indices were stable through this period. We then obtained values for succeeding years by adjusting the 1967-68 average by stock abundance indices based on pre-recruit survey catches (Brown and Hennemuth see footnote 6; Parrack[23]), i.e.,

$$\text{Stock size in year } i = \text{Mean stock size for 1967-68} \times \frac{\text{Abundance index for year } i}{\text{Mean abundance index for 1967-68}} \quad (4)$$

For an estimate of SA 6 stock size, we obtained values for the 1963-66 period by multiplying the computed average stock size value for southern New England by the ratio between mean survey abundance indices between the SA 6 and southern New England stock areas and the ratio between the actual bottom areas considered; we obtained the remaining values using stock abundance indices (Parrack see footnote 23) as above. For the Georges Bank (5Ze) stock, we assumed an F value of 0.8 in 1964 and 1965 (Brown and Hennemuth see footnote 6), calculated stock sizes by Equation (3), and averaged these values to obtain an initial estimate; we then adjusted this value by means of commercial abundance indices (Brown and Hennemuth see footnote 6; Parrack see footnote 23) according to Equation (4) to obtain estimates for later years. The Cape Cod yellowtail stock was considered to have been relatively stable in recent years; we computed an estimate for 1969 by Equation (3) assuming an F value of 0.8 and added the resulting value to each Georges Bank stock size estimate to obtain combined estimates for the Georges Bank area.

We obtained stock size estimates for the remaining stocks from Equation (3) using available estimates of F and M and historical catch data (International Commission for the Northwest Atlantic Fisheries 1965-1973, 1974c, 1975a, see footnote 12). We computed an average stock size for the entire 1965-75 period for 5Y cod using mortality rates reported by Penttila and Gifford[24],

[19]Anderson, E. D. 1975. Assessment of the ICNAF Division 5Y silver hake stock. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1975, Res. Doc. No. 62, Serial No. 3544 (mimeo.), 13 p.

[20]Anderson, E. D. 1975. Assessment of the ICNAF Subdivision 5Ze and Subdivision 5Zw-Statistical Area 6 silver hake stocks. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1975, Res. Doc. No. 94, Serial No. 3574 (mimeo.), 17 p.

[21]Anderson, E. D. 1974. Assessment of red hake in ICNAF Subarea 5 and Statistical Area 6. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1974, Res. Doc. No. 19, Serial No. 3165 (mimeo.), 27 p.

[22]Clark, S. 1975. Current status of the Georges Bank (5Ze) haddock stock. Int. Comm. Northwest Atl Fish. Annu. Meet. 1975, Res. Doc. No. 48, Serial No. 3527 (mimeo.), 9 p.

[23]Parrack, M. L. 1974. Status review of ICNAF Subarea 5 and Statistical Area 6 yellowtail flounder stocks. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1974, Res. Doc. No. 99, Serial No. 3335 (mimeo.), 17 p.

[24]Penttila, J. A., and V. M. Gifford. 1975. Growth and mortality rates for cod from the Georges Bank and Gulf of Maine areas. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1975, Res. Doc. No. 46, Serial No. 3525 (mimeo.), 13 p.

while for 5Z cod we computed an average figure for the 1970-75 period using mortality rates from the above paper and obtained values for the remaining years by adjusting this average by commercial abundance indices reported by Brown and Heyerdahl.[25] We followed an analogous procedure in the case of "other finfish" by computing a value for 1967 (chosen to be in the middle of the period) assuming an F value of 0.4 and $M = 0.2$; we then calculated commercial abundance indices from historical catch data and total effort estimates for SA 5 and 6 (Brown et al. in press) and obtained stock size estimates for the remaining years by adjusting the 1967 value by means of these abundance indices according to Equation (4), as above. For redfish, other flounders, and pollock, we computed average values from Equation (3) using available sustainable yield estimates and assumed values of F, as follows ($M = 0.2$ in all cases):

Species	*Period*	*Sustainable yield estimate (tons × 10^{-3})*	F
Redfish	1964-75	16 (Mayo[26])	0.4
Other flounders	1964-69	25	0.7
Other flounders	1970-75	20	0.9
Pollock	1964-75	[27]16	0.4

Turning to survey abundance indices, an inherent problem in any analysis of trawl data lies in the fact that the computed means and variances are seldom, if ever, independent. The present data are no exception; Grosslein (1971) has found that in the present survey individual stratum variances are approximately proportional to the squares of the stratum means, indicating that a logarithmic transformation is appropriate (Steel and Torrie 1960). Under these conditions, use of a logarithmic scale transformation tends to normalize the data and render means and variances independent, thereby permitting use of parametric statistical methods (obviously, anomalous fluctuations in observed trends are also reduced considerably). Accordingly, we computed stratified mean catch per tow values for all stocks using ln (kilograms + 1) values for each tow; strata sets used are given by species and stock in Table 10. We then computed estimates of stratified mean catch per tow in original units by retransforming as suggested by Bliss (1967:128) according to the relation:

$$E(\bar{y}_{st}) = \exp(\bar{y}_{st} + S^2/2) \quad (5)$$

where $E(\bar{y}_{st})$ represents the estimated (retransformed) stratified mean catch per tow and $\bar{y}_{st}$ and S^2 represent the stratified mean and the estimated population variance, respectively, in logarithmic units, computed as in Equations (1) and (2) above. We also calculated untransformed ($\bar{y}_{st}$) values for the stocks and strata sets in Table 10 for comparative purposes.

After obtaining stock size estimates and abundance indices as described above, we computed catchability coefficients for all years by dividing both untransformed and retransformed stratified mean catch per tow for year i by the appropriate stock size value at the beginning of year $i + 1$ (or by the computed average stock size). Deviations from the arithmetic mean were then plotted by year; where trends were apparent,

TABLE 10.—Strata sets used in computing stratified mean catch per tow values by stock.

Species and stock	Strata sets: Middle Atlantic north[1]	Strata sets: Southern New England north[2]
Cod		
5Y[3]	26-30, 36-40	26-30, 36-40
5Z	5-30, 36-40	5-30, 36-40
Haddock		
5Ze	13-25	13-25
Redfish	18, 22, 26-30, 36-40	1-30, 36-40
Silver hake		
5Y	26-30, 36-40	26-30, 36-40
5Ze	13-25	13-25
5Zw-6	61-76, 1-12	1-12
Red hake		
5Ze	13-25	13-25
5Zw-6	61-76, 1-12	1-12
Pollock	61-76, 1-30, 36-40	1-30, 36-40
Yellowtail		
5Ze	13-25	13-25
5Zw	5-12	5-12
6	69-76, 1-4	1-4
Other flounders	61-76, 1-30, 36-40	1-30, 36-40
Herring		
5Y	26-30, 36-40	26-30, 36-40
5Z-6	63-76, 1-25	1-25
Mackerel	61-76, 1-30, 36-40	1-30, 36-40
Other finfish	61-76, 1-30, 36-40	1-30, 36-40
Short-finned squid	61-76, 1-30, 36-40	1-30, 36-40
Long-finned squid	61-76, 1-30, 36-40	1-30, 36-40

[1]Strata for the Middle Atlantic area (61-76) added in 1967.
[2]Since 1963 (strata 1-40).
[3]Alphanumeric designations refer to divisions and subdivisions of SA 5 and 6 shown in Figure 1.

[25]Brown, B. E., and E. G. Heyerdahl. 1972. An assessment of the Georges Bank cod stock (Div. 5Z). Int. Comm. Northwest Atl. Fish. Annu. Meet. 1972, Res. Doc. No. 117, Serial No. 2831 (mimeo.), 24 p.

[26]Mayo, R. K. 1975. A preliminary assessment of the redfish fishery in ICNAF Subarea 5. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1975, Res. Doc. No. 59, Serial No. 3541 (mimeo.), 31 p.

[27]Pollock in ICNAF Divisions 4VWX, Subarea 5, and Statistical Area 6 are currently considered as a unit stock. Accordingly, this figure represents the SA 5 and 6 proportion of the estimated sustainable yield for this stock as determined from historical catch data.

linear regressions were fitted to the data to evaluate the degree of relationship. A significant ($P<0.01$) negative trend was obtained for haddock for both untransformed and retransformed data (Figure 11). This could have resulted from overestimates of stock size in later years or actual differences in catchability associated with changing availability as stock size decreased. A plot of numbers captured per tow by year during the period of study suggested that actual differences in catchability may have occurred (Figure 11); accordingly, we divided the period of study into two units (1963-68 and 1969-74) for the purpose of calculating weighting coefficients for the species. The dividing line was taken as the point in which the percentage of tows containing five haddock or less reached 90%.

In the case of species for which more than one stock had been defined, some question existed as to whether coefficients should be computed for the entire species or on a stock basis. As no consistent trends had been found for these species over time, one-way analysis of variance was used to test for differences between stocks, using years as replicate observations. These tests revealed significant differences ($P<0.05$) between individual stocks for all species except yellowtail (i.e., cod, silver and red hake, and herring). We therefore retained individual stocks as discrete units in computing biomass declines (i.e., no attempt was made to combine stocks on a species basis).

After obtaining the desired sets of catchability coefficients for all stocks, we obtained weighting coefficients by calculating arithmetic means of untransformed and retransformed sets (Tables 11, 12), using the entire set except in the case of haddock as explained above. We then computed biomass estimates by year, viz.

TABLE 11.—Weighting coefficients calculated by stock from untransformed and retransformed survey data, 1967-74, Middle Atlantic, southern New England, Georges Bank, and Gulf of Maine area (strata 61-76, 1-30, and 36-40).

Species and stock[2]	Calculated from: Untransformed data — Weighting coefficient[3]	Untransformed data — Coefficient of variation[4]	Retransformed data[1] — Weighting coefficient[3]	Retransformed data[1] — Coefficient of variation[4]
Cod:				
5Y	39.954	0.31	44.545	0.44
5Z	5.160	0.52	3.433	0.50
Haddock[5]:				
5Ze	14.146, 10.193	0.25, 0.46	15.591, 7.461	0.71, 0.56
Redfish	40.063	0.29	49.188	0.32
Silver hake:				
5Y	8.714	0.80	8.348	0.94
5Ze	0.727	0.30	0.650	0.31
5Zw-6	1.325	0.33	1.101	0.40
Red hake:				
5Ze	6.565	0.65	5.384	0.74
5Zw-6	2.341	0.74	1.422	0.71
Pollock	4.069	0.45	1.442	0.37
Yellowtail:				
5Ze	17.391	0.24	15.106	0.31
5Zw	45.722	0.79	42.229	0.70
6	67.795	0.95	39.969	0.76
Other flounders	10.897	0.18	11.134	0.17
Herring:				
5Y	0.125	>1.0	0.039	0.97
5Z-6	0.010	>1.0	0.002	0.75
Mackerel	0.015	>1.0	0.005	0.57
Other finfish	12.809	0.31	14.553	0.14
Short-finned squid	0.302	0.37	0.206	0.34
Long-finned squid	5.240	0.46	4.302	0.65

[1]Estimated stratified mean catch per tow values computed from transformed data according to the relation, $E(\bar{y}_{st}) = \exp(\bar{y}_{st} + S^2/2)$, where $\bar{y}_{st}$ and S^2 represent the mean and estimated population variance, respectively, on the transformed scale.

[2]Weighting coefficients calculated by individual stock for cod, haddock, silver hake, red hake, yellowtail, and herring; stock areas are given in Figure 1. Stock areas for the remaining species are equivalent to all strata in SA 5 and 6 covered during 1967-74.

[3]Weighting coefficients calculated as $\frac{\sum_{i=1}^{n}\left[C_i/S_{i+1}\right]}{n}$ where C_i = stratified mean catch per tow (tons) in year i and S_{i+1} = stock size at the beginning of the following year. All values $\times 10^8$.

[4]Coefficient of variation calculated over all years.

[5]Weighting coefficients computed separately for 1967-68 and 1969-74 data due to apparent changes in catchability.

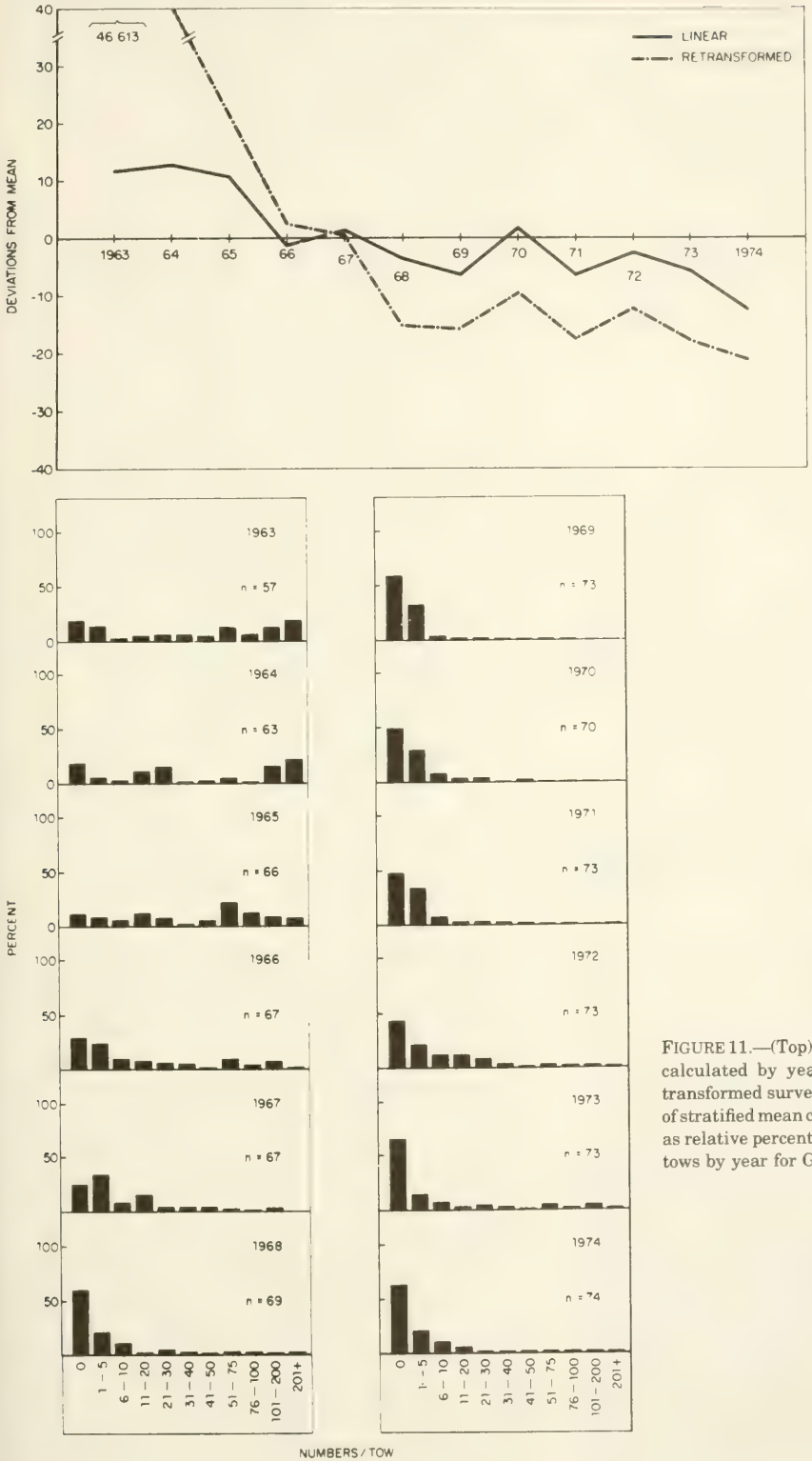

FIGURE 11.—(Top) Trends in catchability coefficients calculated by year using untransformed and retransformed survey data, and (bottom) distributions of stratified mean catch per tow in numbers expressed as relative percentages of the total number of survey tows by year for Georges Bank haddock.

TABLE 12.—Weighting coefficients calculated by stock from untransformed and retransformed survey data, 1963-74, southern New England, Georges Bank, and Gulf of Maine area (strata 1-30 and 36-40).

Species and stock[2]	Calculated from: Untransformed data — Weighting coefficient	Untransformed data — Coefficient of variation[4]	Retransformed data[1] — Weighting coefficient	Retransformed data[1] — Coefficient of variation[4]
Cod:				
5Y	42.877	0.31	41.000	0.41
5Z	4.918	0.46	3.462	0.47
Haddock[5]:				
5Ze	20.696, 10.193	0.36, 0.46	38.857, 7.461	0.63, 0.56
Redfish	42.776	0.41	46.898	0.34
Silver hake:				
5Y	7.948	0.79	8.205	0.94
5Ze	0.814	0.49	0.724	0.46
5Zw-6	2.122	0.32	2.116	0.37
Red hake:				
5Ze	6.503	0.69	5.380	0.77
5Zw-6	3.644	0.68	3.070	0.62
Pollock	5.174	0.41	2.279	0.46
Yellowtail:				
5Ze	17.143	0.28	15.221	0.38
5Zw	39.399	0.77	40.716	0.62
6	104.145	>1.00	121.231	>1.00
Other flounders	13.016	0.22	14.293	0.25
Herring:				
5Y	0.178	>1.00	0.095	>1.00
5Z-6	0.027	>1.00	0.005	0.94
Mackerel	0.015	>1.00	0.006	0.56
Other finfish	12.569	0.31	13.648	0.18
Short-finned squid	0.254	0.70	0.177	0.63
Long-finned squid	3.124	0.80	2.099	>1.00

[1]Estimated mean catch per tow values computed from transformed data according to the relation, $E(\bar{y}_{st}) = \exp(\bar{y}_{st} + S^2/2)$, where $\bar{y}_{st}$ and S^2 represent the mean and estimated population variance, respectively, on the transformed scale.

[2]Weighting coefficients calculated by individual stock for cod, haddock, silver hake, red hake, yellowtail, and herring; stock areas are given in Figure 1. Stock areas for the remaining species are equivalent to all strata in SA 5 and 6 covered during 1967-74

[3]Weighting coefficients calculated as $\dfrac{\sum_{i=1}^{n}\left[C_i/S_{i+1}\right]}{n}$ where C_i = stratified mean catch per tow (tons) in year i and S_{i+1} = stock size at the beginning of the following year. All values $\times 10^8$.

[4]Coefficient of variation calculated over all years.

[5]Weighting coefficients computed separately for 1967-68 and 1969-74 data due to apparent changes in catchability.

$$\sum_{j=1}^{k}\left[C_{ij}/W_j\right] \quad \text{for all } i \qquad (6)$$

where C_{ij} refers to stratified mean catch per tow for the jth stock in the ith year and W_j refers to the weighting coefficient for the jth stock (Tables 13, 14), summation being over k stocks. For the purposes of this paper, we consider each computed estimate as representing stock size at the beginning of the year following collection of the survey data ($i + 1$), as catchability coefficients were calculated by relating catch per tow values in autumn of year i to stock size at the beginning of year $i + 1$ (above). Note that with the exception of 1970 figures for "all data" (Tables 13, 14), values computed from retransformed data agree reasonably well with those computed from untransformed values; consequently the general appropriateness of assuming a lognormal distribution for these data is confirmed.

The average stock size estimate for 1964-66 obtained for all species of 5.0×10^6 tons (Table 14) is almost identical to that obtained by Edwards (1968) for the same area and period (5.1×10^6

TABLE 13.—Stock size estimates (tons $\times 10^{-3}$) for ICNAF Subarea 5 and Statistical Area 6, 1967-74, Middle Atlantic, southern New England, Georges Bank, and Gulf of Maine, inclusive (strata 61-76, 1-30, and 36-40).

Year	Calculated with: Untransformed data — All data	Untransformed data — Data for principal pelagics excluded	Retransformed data — All data	Retransformed data — Data for principal pelagics excluded
1968	7,481	1,783	8,012	1,806
1969	3,826	1,795	5,209	1,880
1970	9,555	1,859	5,158	1,750
1971	2,097	1,567	2,964	1,736
1972	3,156	1,331	3,062	1,418
1973	3,136	1,870	3,661	1,825
1974	2,098	1,841	2,541	1,760
1975	1,828	1,107	1,934	1,119

TABLE 14.—Stock size estimates (tons × 10^{-3}) for ICNAF Subarea 5 and Statistical Area 6, 1963-74, southern New England, Georges Bank and Gulf of Maine, inclusive (strata 1-30 and 36-40).

	Calculated with			
	Untransformed data		Retransformed data	
Year	All data	Data for principal pelagics excluded	All data	Data for principal pelagics excluded
1964	6,616	3,317	7,357	3,640
1965	2,780	2,373	2,677	2,151
1966	5,079	2,088	5,382	2,184
1967	8,331	1,610	7,770	1,605
1968	6,056	1,478	6,431	1,493
1969	3,400	1,787	4,238	1,763
1970	11,490	2,012	5,158	1,867
1971	2,174	1,642	2,828	1,759
1972	2,644	1,411	2,751	1,501
1973	3,231	1,964	3,622	1,937
1974	2,371	2,009	2,717	1,931
1975	2,036	1,217	1,981	1,165

tons). Edwards obtained biomass estimates by adjusting minimum biomass figures for each species by a factor accounting for differences in availability and vulnerability, and although estimates obtained for individual species by these methods differed in certain cases it can be seen that, on the average, results are quite comparable.

The data of Tables 13 and 14 again reveal pronounced declines. In Table 13 (1968-75, all strata) comparisons of averages for "all data" between 1968-69 and 1974-75 reveal a 65% decline for untransformed data and a 66% decline in the case of retransformed values; with principal pelagics excluded, the corresponding figures are 18 and 22%, respectively. In Table 14 (1964-75, Middle Atlantic strata excluded) comparisons between averages for "all data" for 1964-66 and 1973-75 reveal declines of 47% and 46% for untransformed and retransformed values, respectively, while with principal pelagics excluded the corresponding figures were 33% and 37%. The greater decrease for the 1968-75 period for "all data" might appear somewhat anomalous but actually results primarily from appearance of the outstanding 1967 mackerel year class.

As the estimates in Tables 13 and 14 purport to measure declines in biomass in SA 5 and 6, it might logically be argued that they could be combined in some way (use of the 1968-75 data would be preferable in that survey coverage extended further to the south). Paired *t*-tests indicated no differences between corresponding stock size estimates in Tables 13 and 14 for the 1968-75 period. Therefore, we combined the 1968-75 estimates in Table 13 with the 1964-67 estimates in Table 14 (Figures 12, 13) and computed percentage changes between the means of the 1964-66 and 1973-75 periods, as before. For "all data," we obtained declines of 51% and 47% with untransformed and retransformed values; with herring and mackerel excluded, the corresponding figures were 38% and 41%.

Analysis of both untransformed and retransformed data yield essentially similar results. The data of Figures 12 and 13 illustrate the effectiveness of the transformation in reducing anomalies caused by variability in the data. For untransformed estimates (Figure 12) it will be

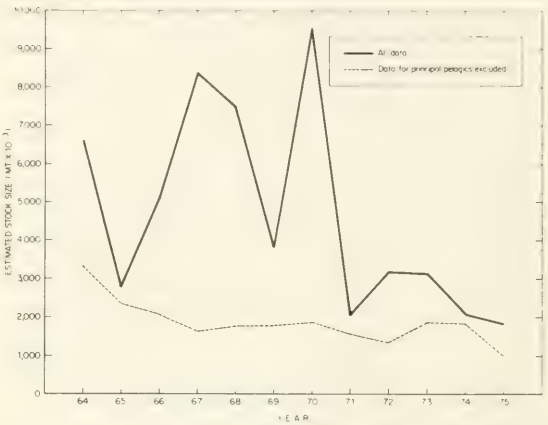

FIGURE 12.—Estimates of fishable biomass by year for ICNAF Subarea 5 and Statistical Area 6, 1964-75, calculated with untransformed survey data. Curves were plotted by combining 1968-75 estimates from Table 13 with 1964-67 estimates from Table 14.

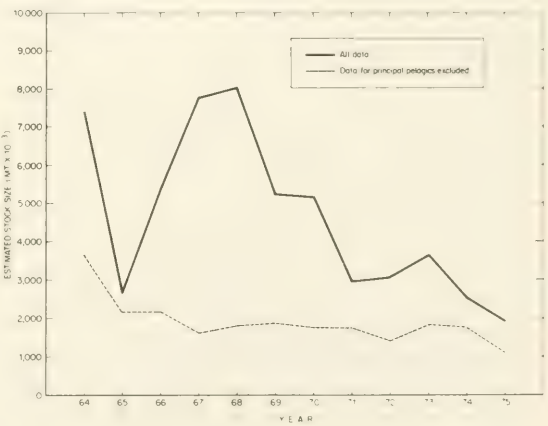

FIGURE 13.—Estimates of fishable biomass by year for ICNAF Subarea 5 and Statistical Area 6, 1964-75, calculated with retransformed survey data. Curves were plotted by combining 1968-75 estimates from Table 13 with 1964-67 estimates from Table 14.

noted that an anomalous peak occurs in 1970, which examination of biomass estimates on a per-species basis revealed to have been caused by anomalously high mackerel catches in certain tows during the 1969 survey. The influence of this factor appears to have been compensated for by use of the logarithmic transformation (Figure 13). On the other hand, the anomalously low data point for 1965 (Figures 12, 13) appears to have been caused by anomalously low catches of herring in that year, a circumstance in which the transformation was ineffective. It does appear, however, that by and large the transformation was of definite value in following trends through time, although estimates for most of the years considered proved to be similar.

The above analyses clearly indicate that biomass levels have decreased significantly in SA 5 and 6 in recent years; the trend observed correlates well with increases in fishing effort observed by Brown et al. (in press). In addition, we have also found evidence indicating that major changes in species composition have occurred as well. The apparent increase in white hake abundance in the Gulf of Maine in recent years (Table 5) could have resulted from population increases in response to reductions in other groundfish species. Similarly, increased mackerel abundance coincident with declining abundance of herring (Tables 3, 4) may indicate some form of species interaction coincident with exploitation, while apparent increases in abundance of squid (Tables 2-7, Figure 9) may have occurred in response to declining abundance of finfish species. The relationships involved are unclear at present and further study is obviously necessary.

Comparisons of annual landings data since 1971 (over 1.0×10^6 tons) with biomass estimates in Tables 13 and 14 indicate that the fraction of the biomass harvested annually has increased significantly in recent years (i.e., from less than one-fifth of the total in the early and mid-1960's to between one-third and one-half of the total at present). Furthermore, landings since 1971 have exceeded the composite MSY figure of 950×10^3 tons calculated by Brown et al. (in press) based on the Schaeffer yield model. This information, together with declines in stock size approximating 50% as indicated in this paper, imply that a significant degree of overfishing has occurred and that stock size has been reduced below the level corresponding to MSY. Back-calculations for all species in Tables 13 and 14 provide an average stock size estimate of approximately 7.0×10^6 tons prior to 1964, from which (allowing for the U.S. coastal fishery in previous years) it may be inferred that the actual virgin biomass for this fishery probably approximated $8.0\text{-}9.0 \times 10^6$ tons. Since the Schaeffer yield model postulates that MSY will be taken at a stock level corresponding to one-half the maximum (Schaeffer 1954), we may in turn assume that a stock level of approximately $4.0\text{-}4.5 \times 10^6$ tons should be maintained for SA 5 and 6 if MSY from this resource is to be achieved. In contrast, estimates for fishable biomass in the present paper approximate 2.0×10^6 tons at the start of 1975, implying that a lengthy period of reduced exploitation is necessary if stocks are to be rebuilt to the MSY level.

In April 1975, the Assessments Subcommittee (STACRES) reviewed evidence relating to declines in biomass in SA 5 and 6 in recent years and concluded that substantial reductions in catch would be necessary if stocks are to recover (International Commission for the Northwest Atlantic Fisheries 1975c). Accordingly, a TAC of 650×10^3 tons was recommended to ICNAF and approved at the Seventh Special Commission Meeting (International Commission for the Northwest Atlantic Fisheries 1975b) in September. Even with a reduction of this magnitude, STACRES estimated that a minimum of 7 yr would be required for this resource to recover to the MSY point.

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LARVAL TRANSPORT AND YEAR-CLASS STRENGTH OF ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*[1]

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ABSTRACT

A Ricker spawner-recruit model was developed for Atlantic menhaden, *Brevoortia tyrannus*, from data on the 1955-70 year classes. The number of eggs produced by the spawning stock was calculated as the independent variable to account for changes in fecundity due to changes in population size and age structure. A survival index was developed from deviations around the Ricker curve and was regressed on several environmental parameters to determine their density-independent effects. The recruit-environment model accounted for over 84% of the variation in the survival index. Zonal Ekman transport, which acts as a mechanism to transport larval menhaden from offshore spawning areas to inshore nursery grounds, was the most significant parameter tested. Ricker functions for good and poor environmental years were developed, indicating the wide range of recruitment that can be expected at different stock sizes. Comparisons of spawner-recruit relations for Pacific sardine and Atlantic menhaden indicated striking similarities. Surplus yield for the Atlantic menhaden fishery was calculated from observed and predicted survival, and compared with the actual performance of the fishery.

One of the more intriguing and important problems in fishery science, that of the relative influence of spawning stock size and environmental variation on year-class strength, has resulted in a long-standing controversy among fishery biologists. The two principal reasons for investigating the effects of stock size and environmental change on year-class strength are, of course, to understand what has happened and to predict what will happen. Since environmental conditions will produce varying recruitment at a given stock size, one must determine both the reproductive potential under average environmental conditions, i.e., the density-dependent spawner-recruit curve, and the effect of varying environmental conditions, or the density-independent function. The difficulty comes, as Clark and Marr (1955) point out, in separating the relative influences of the two functions. A prerequisite for such an attempt is a reliable long-term series of data, adequate to estimate the size of the spawning stocks, the number of recruits, the age structure of the populations, the patterns of environmental variation, and the rate at which the resource is being harvested.

Biologists are in general agreement that the most critical survival period for many marine fishes is during the time of egg and larval drift. Major factors affecting survival during this period are food (Cushing 1969), cannibalism by filter-feeding parents (Radovich 1962; Murphy 1967), and ocean currents (Sette 1943). The first two of these factors are density dependent and tend to control population growth. Transport by ocean currents to or from areas favorable to survival is density independent and has been used to explain successful year classes of Atlantic mackerel by Sette (1943) and Atlantic haddock by Walford (1938). A relationship between winds and year-class success for the East Anglian herring fishery was reported by Carruthers (1938). Cushing (1969) pointed out that ". . . correlations between recruitment and winds were often successful for a period of years, after which they failed catastrophically."

Other density-independent factors, such as temperature, particularly in the sense of long-term climatic change, have been related to changes in spawning success and location. For example, a change in the environment of the Pacific sardine over a period of time which resulted in a change in normal distribution patterns and a series of poor year classes was postulated by Radovich (1962). Sissenwine (1974) documented a significant relationship between atmospheric temperature and the recruitment and equilibrium catch of yellowtail flounder, but did not explain

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the mechanism by which temperature anomalies influence the fishery.

Cushing (1969) listed three sources of variation which might affect recruitment: year-to-year environmental changes, larger scale climatic changes, and differences due to stock density. The year-to-year effects were considered by Cushing to be randomly distributed around the stock and recruitment curve and not of major consequence in the long-term regulation of fisheries. Over a number of years, variations around a stock and recruitment curve may tend to cancel one another and the fishery may provide a relatively stable yield. However, when a fishery is overexploited and subjected to poor survival as a result of environmental conditions, stock size may be reduced to a small fraction of that necessary to maintain a maximum sustainable yield (MSY). Further, with overcapitalization, fishing effort may remain high, preventing a resurgence of the stocks by maintaining a spawning stock too small to produce a large year class under favorable environmental conditions. From this standpoint, a predictive capability, based on knowledge of density-dependent and density-independent recruitment could be vital to the maintenance of adequate stock size through a reduction in effort, or to the harvesting of surplus population beyond that necessary to maintain the MSY. Fisheries, in the generic sense, operate over long periods of time. Fishermen, fish processors, and consumers operate on a much shorter time scale and large, unexpected, year-to-year fluctuations in stock size have significant economic and social impact.

The Atlantic menhaden, *Brevoortia tyrannus,* is a species that has supported a significant fishery since the middle of the 19th century (Reintjes 1969). Landings from the fishery have been sampled extensively since 1955 and the major characteristics of the stocks and the fishery have been determined. Information for a variety of stock sizes and from a range of environmentally different years is available, and the stocks have been subjected to heavy fishing pressure (Schaaf and Huntsman 1972).

A study of forecasting methods and the development of a forecast for the Atlantic menhaden fishery was carried out by the National Marine Fisheries Service (Schaaf et al.[4]). The manuscript points out that knowledge of the biology of recruitment of the Atlantic menhaden is needed to take advantage of strong year classes through the development of short-term fishing strategies. Knowledge of poor year classes would also be beneficial from a standpoint of avoiding excessive fishing pressure on the stocks.

A single year class is harvested by industry over a 4- to 5-yr period, and its failure could be masked to some extent by overfishing of other year classes taken concurrently, resulting in serious stock depletion. Conversely, a large year class may lead to a large increase in fishing effort which continues after the year class has been harvested, leading to overcapitalization and overfishing in subsequent years of reduced stock size. A large year class, followed by several poor year classes is potentially disastrous to the fishing industry and to the stocks. Knowledge of the recruitment process and the ability to predict year-class strength is necessary if the fishery is to operate at the MSY level.

Detailed information on the composition of Atlantic menhaden stocks obtained yearly since 1955 shows a range in numbers recruited into the fishery of from 11.5 billion in 1958 to 0.9 billion in 1967. Although some of the variation in recruitment can be attributed to fluctuations in the size of the spawning stock (Schaaf and Huntsman 1972), the wide range of fluctuations between years with similar spawning stock sizes suggests that environmental factors are influencing the survival of prerecruits. This study attempts to identify those factors, determine their relative influences, and develop a predictive model to account for the variations between actual and expected recruitment into the Atlantic menhaden fishery.

SPAWNING AND LARVAL DISTRIBUTION

Gravid or running-ripe Atlantic menhaden are rarely caught and spawning has not been observed. Without conclusive information, the time and place of spawning has been inferred by the relative ripeness of maturing ova, the occurrence of partially spent ovaries, and the distribution and occurrence of eggs and small larvae.

Higham and Nicholson (1964:262) reported that

[4]Schaaf, W. E., J. E. Sykes, and R. B. Chapoton. 1973. Forecast of 1973 Atlantic and Gulf menhaden catches based on the historical relation of catch and fishing effort. Unpubl. manuscr., 22 p.

Atlantic Estuarine Fisheries Center, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

"... (only 11 specimens containing numerous ripe ova were encountered in the routine field examination of several hundred thousand fish during 4 years of sampling), ..." Based on a sample of approximately 37,000 female menhaden from all Atlantic coast fishing areas, they concluded, p. 270, "Spawning apparently occurred in the North Atlantic Area [north of Long Island] from May to September; in the Middle Atlantic [south to Cape Hatteras], from March through May and again in September and October; and in the South Atlantic [south of Cape Hatteras], from October through March." Based on the percentages of sexually active (ripening but not ripe) females in their samples, it appears that a majority of spawning activities take place in the South Atlantic Bight. The spawning cycle appears to be one of limited spawning during a spring northward migration, limited early and late summer spawning as far north as Cape Cod and occasionally into the Gulf of Maine, increased spawning activity during a southward fall migration, and intensive (90-100% sexually active) winter spawning in the South Atlantic Bight.

Spawning activities through the winter are difficult to determine because the stocks move offshore and there is no fishery for menhaden during that period. This is the only time during the year that menhaden schools are not available in coastal waters, and that fact leads to speculation about an offshore spawning migration.

Available information about the distribution of menhaden eggs and larvae has been reviewed by Kendall and Reintjes (1975) and Chapoton.[5] Inferences regarding spawning activities have been drawn from various surveys of restricted time and coverage which have been conducted on the east coast since 1937 (Permutter 1939), primarily in sounds, bays, and creeks. Only two egg and larval research efforts have provided large-scale systematic coverage of major menhaden spawning areas on the Atlantic coast. Those are the cruises of the MV *Theodore N. Gill* (Reintjes 1961) and the RV *Dolphin* (Kendall and Reintjes 1975). The distribution of larvae collected by the *Dolphin* cruises is in general agreement with the spawning cycle documented by Higham and Nicholson (1964). RV *Dolphin* cruises covered the entire continental shelf from Cape Lookout, N.C., to Martha's Vineyard, Mass., in 14 transects from December 1965 to May 1966.

The southern part of the menhaden spawning range was covered by cruises of the *Theodore N. Gill* in 1953 and 1954 (Reintjes 1961). The absence of menhaden larvae during all but the winter cruises led Reintjes to conclude that menhaden spawn along the south Atlantic coast generally from December to February. The southern limit of the spawning range of the Atlantic menhaden is undetermined because a southerly species, the yellowfin menhaden, *Brevoortia smithi,* has an overlapping spawning range. Those larvae collected by the *Theodore N. Gill* off southern Florida were probably *B. smithi* and those collected off Cape Lookout, the other area of larval concentration located by the *Theodore N. Gill,* were undoubtedly *B. tyrannus.* Based on the distribution of juveniles and adults, it seems safe to assume that Atlantic menhaden spawn as far south as northern Florida, but at a low intensity in the extreme southern part of their range. Reintjes (1969) hypothesized that much of the spawning takes place south of Cape Hatteras.

Atlantic menhaden appear to spawn over most of the continental shelf. The general timing sequence and location of spawning during migrations indicates that eggs and larvae are subjected to an open ocean environment for a sufficient length of time to be affected by oceanic conditions. Both the *Dolphin* and *Theodore N. Gill* cruises resulted in catches of small larvae from nearshore to the edge of the shelf. *Dolphin* records show a general increase in average size of larvae from offshore to inshore stations as well as increased distance offshore from north to south. Major summer spawning in the New York-New England area appears to occur well inshore, and large numbers of eggs and larvae have been taken in bays and sounds from Long Island north. Matthiessen (1974) reported concentrations of eggs that exceeded 20,000/100 m^3 in June 1972 in Narragansett Bay, R.I., and computed the total production of eggs in the Bay during the summer of 1973 as being in excess of 4.64×10^{11}.

Concentrations of eggs and small larvae are found progressively nearer the offshore edge of the shelf during the fall and winter southward migration. Massmann et al. (1962) found larvae as small as 7 mm 79 km off Chesapeake Bay, and concluded that spawning and hatching occurred more than that distance offshore. Reintjes (1968) reported an extensive patch of menhaden eggs in Onslow Bay,

[5]Chapoton, R. B. 1972. On the distribution of Atlantic menhaden eggs, larvae, and adults. Unpubl. manuscr., 69 p. Atlantic Estuarine Fisheries Center, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

N.C., in December 1966, 40 km from shore and estimated their age at 8 to 55 h. *Theodore N. Gill* cruises resulted in the location of larval menhaden up to 220 km off Cape Fear, N.C., in February 1954, although most larvae taken during the *Gill* cruises were over the shelf. Cruises of the RV *Undaunted* during the winter of 1970-71 also yielded larvae 170-175 km off Cape Fear.

PHYSICAL OCEANOGRAPHY OF THE SPAWNING REGION

An excellent summary of the oceanography of the coastal waters of the U.S. east coast was recently prepared by Bumpus (1973) and the reader is referred to that for detailed information. Bumpus identified three distinct subdivisions as the Gulf of Maine, Middle Atlantic Bight (Cape Cod to Cape Hatteras), and South Atlantic Bight (Cape Hatteras to Cape Canaveral). Although menhaden are periodically taken north of Cape Cod, Mass., migratory intrusions do not occur there routinely and the area is not one of significant menhaden spawning activity. A brief summary of oceanographic conditions in the other two regimes of significant menhaden spawning activities follows.

In the Middle Atlantic Bight the Gulf Stream diverges abruptly toward the northeast, passing Cape Hatteras, and the space between the Shelf Water masses and the Gulf Stream left by this divergence is occupied by the Slope Water mass. Flow in the Shelf Water and Slope Water is generally slow and southward, more or less parallel to the isobaths except for portions of the Slope Water mass near the Gulf Stream which have a northward to northeastward motion imparted by transfer of momentum from the Gulf Stream. At Cape Hatteras the southward flowing waters generally turn to flow northward and an unknown fraction of these waters becomes entrained within the Gulf Stream. The southward drift of Shelf Water is partly driven by the pressure field developed around river effluent plumes, and in times of low runoff and southeasterly winds the flow may be reversed. Menhaden spawning takes place throughout the Middle Atlantic Bight and oceanographic conditions there should have a major influence on the distribution and survival of eggs and larvae.

In the South Atlantic Bight the Gulf Stream current forms the seaward boundary of the region of intensive Atlantic menhaden spawning. The current's mean position is parallel to and a short distance (37-74 km in Carolina coastal waters) from the edge of the continental shelf (180-m isobath). A mass of Shelf Water which has lower salinity and lower temperature, except in summer, than the Gulf Stream water is found shoreward of the Gulf Stream. Motion of the Shelf Water mass is generally slow and variable, responding to local winds, but not customarily flowing southward, unlike the pattern of flow of the Shelf Water in the Middle Atlantic Bight. Occasionally southward flows have been identified near the coast, and the cuspate formations of Raleigh Bay, Onslow Bay, and Long Bay suggest southward flow nearshore as part of a large counterclockwise eddy in each bay. The existence of these eddies, although suspected, never has been conclusively demonstrated. Stefansson et al. (1971) found, based on geopotential topography from six cruises in 1966-67, that there was always an indication of a counterclockwise eddy in Onslow Bay. The pattern found in Raleigh Bay was less permanent and influenced by the influx of Virginian Coastal Water from the north.

LARVAL TRANSPORT

Menhaden larvae, spawned offshore, move into estuaries before metamorphosing to juveniles, after traversing long, open ocean distances. The larvae are 18-22 mm in length when they enter estuaries after an oceanic phase of 1½ to 2 mo. Very few small larvae (<12 mm) have been taken in estuaries along the central and southern U.S. Atlantic coast, even though eggs and young larvae have occasionally been taken near shore. The timimg of larval entrance is apparently controlled to some extent by the larvae and is somewhat independent of water movement. During earlier larval stages, however, there is a passive drift period in which larval movement is the result of ocean currents. Based on the rate of fin development, the completely passive phase probably ends when a length of 10-12 mm is reached. Depending on water temperature, menhaden reach that length in 30-45 days (William F. Hettler pers. commun., Atlantic Estuarine Fisheries Center).

Currents with an onshore component, particularly during the passive larval phase, would seem to be important for transportation of the larvae from offshore spawning areas to estuarine nursery grounds. There are no documented

physiological requirements for estuarine dependence, but metamorphosing larvae are rarely taken in the ocean, indicating that apparent requirements (food, shelter, etc.) provided by estuaries are essential in the life cycle of menhaden. Transport to the vicinity of estuaries should increase the opportunity for entering nursery grounds, resulting in good year classes from years of strong onshore transport. Weak onshore transport or water movement offshore would increase the distance that must be actively traversed, reduce chances of survival, and result in a poor year class. If variation in survival is due to variation in the efficiency of transport of larval menhaden from offshore areas to estuaries, then knowledge of the transport mechanisms would be useful for understanding and predicting variation in year-class strength.

Menhaden larvae have been found to be more abundant in the upper 15 m of the water column than in the underlying 18-33 m in extensive surveys of our Atlantic shelf waters (Kendall and Reintjes 1975; Chapoton see footnote 5). It is assumed, therefore, that they remain in the upper mixed layer and are transported along with it. Horizontal transport in the surface layer is principally the result of extensive quasi-steady-state currents and local, variable currents, which are strongly influenced by wind and run-off. Steady state currents, by definition, cannot be responsible for year-to-year variation in larval transport and recruitment, so attention was first turned to the local, variable currents which are superimposed on the quasi-steady-state circulation of the surface layer.

In the search for a westward transport mechanism which varies seasonally and from year-to-year, wind drift data computed from mean monthly atmospheric pressure distributions for the period 1946 to the present were considered first. In particular, plots of zonal (eastward or westward) wind-driven (Ekman) transport produced by the Pacific Environmental Group, NMFS, NOAA were studied (for method see Bakun 1973). A grid point (lat. 35°N, long. 75°W) located about 56 km southeast of Cape Hatteras was selected as being representative of the wind field in the area of interest. The seasonal variation of Ekman transport at lat. 35°N, long. 75°W generally includes relatively strong WSW-SW-SSW transport during the first quarter of each year. Because of the SW-NE trend of the coastline south of Cape Hatteras, Ekman transports significantly west of southwestward (those with a stronger westward component) would be most effective in transporting eggs and larvae toward estuarine nursery areas. Plots of the monthly zonal transport at this point revealed conditions of eastward or weak westward transport during most of the year, shifting to moderate or strong westward transport during January-March; a periodicity which matched that of spawning of menhaden south of Cape Hatteras (Figure 1).

In coastal waters of the Middle Atlantic Bight between Virginia and Long Island, N.Y., computations of monthly zonal Ekman transport exhibited a pattern similar to that found south of Cape Hatteras. Monthly zonal Ekman transport values computed for this area show that stronger westward transport generally occurs in the November-February period of menhaden spawning activities, possibly providing a mechanism for transporting menhaden larvae into the vicinity of estuarine environments.

A model of the circulation of the shelf waters off the Chesapeake Bight was developed and cited for its application to menhaden year-class strength by Harrison et al. (1967). The model was used in an attempt to explain the difference in "production of young menhaden" in Chesapeake Bay from the 1958 year class, an unusually productive one, and the 1964 year class, which was well below average. The model yielded inappropriate surface current regimes to explain strong shoreward larval transport in 1957-58, and Harrison et al. chose near-bottom currents, which appeared more favorable, as an explanation. As cited earlier, data collected in comparative net tows indicate that menhaden larvae are more abundant in the upper layer than the near-bottom layer, a condition which weakens the premise on which the argument is based.

Application of the Ekman drift data to the problem of explaining the large difference in menhaden production in Chesapeake Bay in 1958 and 1964 leads to a more satisfactory biological conclusion than the bottom-layer-transport model used by Harrison et al. (1967). The average monthly westward Ekman transports for the November-March period at two points in the Middle Atlantic Bight for 1957-58 (Table 1) were about twice as large as those for 1963-64, qualitatively implying that variation in wind-driven surface layer transport of larvae may be at least partly responsible for the amount of variation in menhaden year-class strength.

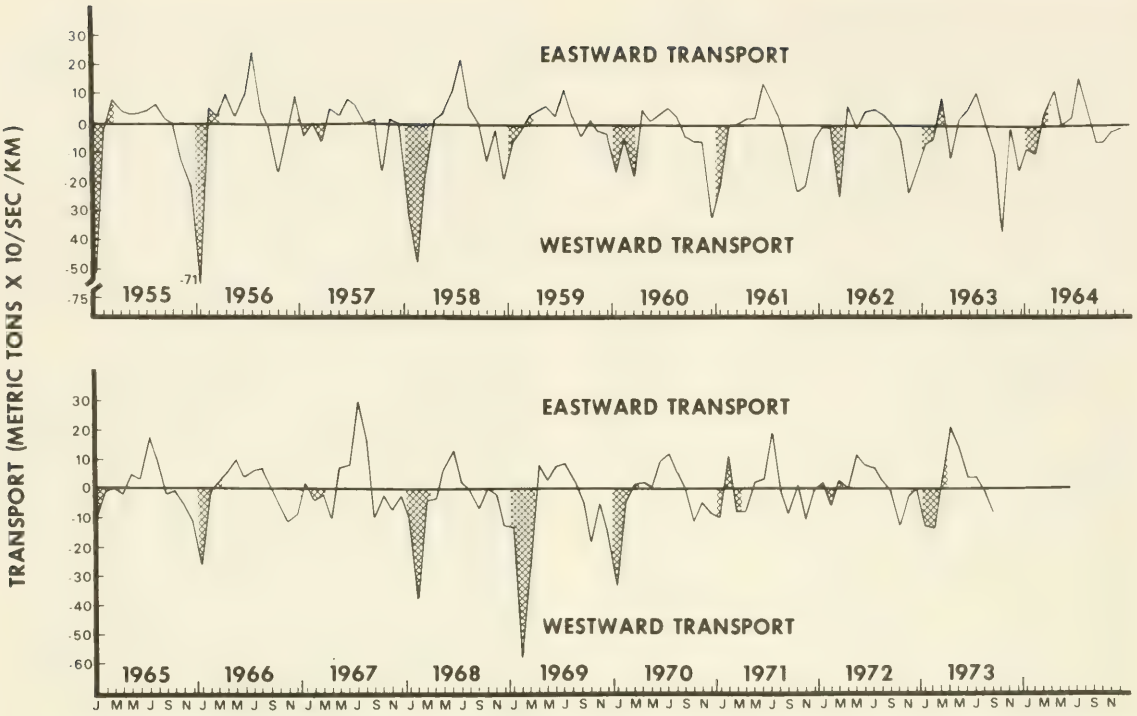

FIGURE 1.—Monthly average zonal Ekman transport at lat. 35°N. long. 75°W, 1955-73. January-March spawning period is shaded.

TABLE 1.—Average westward wind-driven Ekman transport computed for November-March 1957-58 and 1963-64 at lat. 39°N, long. 72°W and lat. 39°N, long. 75°W. Transports expressed in metric tons per second per kilometer of front.

Year	Lat. 39°N, long. 72°W	Lat. 39°N, long. 75°W
1957-58	480	520
1963-64	250	260

SPAWNER-RECRUIT RELATION

Over the 16 yr from 1955 to 1970, there was a sharp decline in the size of the Atlantic menhaden spawning stock and the size of resultant year classes. From 1964 to 1970, the annual catch of spawning age fish averaged only 14% of the previous 9 yr. Resultant per-year recruitment from 1964-70 averaged 42% of that for the previous 9 yr (Schaaf 1972). A description of the average relationship between spawning stock size and recruitment is useful for examining this coincident reduction and for predicting the expected fate of the fishery under different exploitation regimes. A stock-recruit function is also the necessary starting point for developing an index of survival (observed recruitment to that expected from number of spawners) against which one may assess the impact of density-independent environmental effects of recruitment. The approach in this study has been to determine if selected density-independent environmental factors could explain deviations from a postulated spawner-recruit model.

Ricker's (1954) comprehensive study of stock-recruitment formulated a dome-shaped model, with strong compensation, resulting in decreased recruitment at stock sizes beyond some maximum value. It is described by the equation:

$$R = Se^{(S_r - S)/S_m}$$

where R = recruitment
S = spawning stock
e = base of natural logarithm
S_r = maximum equilibrium stock
S_m = stock size yielding maximum absolute recruitment.

Ricker's model states that some stock size (S_m) produces maximum recruitment, and that, because of density-dependent mortality and growth,

stocks greater than S_m produce progressively fewer recruits. There is a size-dependent fecundity relationship for Atlantic menhaden (Higham and Nicholson 1964), and growth rates are slower for large year classes (Gene R. Huntsman, pers. commun., Atlantic Estuarine Fisheries Center). Also, adult menhaden are indiscriminate filter feeders and are known to ingest their own eggs. Calculation of a density-dependent index for Atlantic menhaden (i.e., the slope of a regression of $\ln R$ on $\ln S$) yields a value of 0.238. This index falls within the category described by Cushing (1971) as having a slightly convex spawner-recruit curve. The average fecundity of Atlantic menhaden (113,000 eggs per female) calculated from data used in this study, also places the species in groups which Cushing describes as having a dome-shaped spawner-recruit curve. Accordingly, the Ricker model has been used in this analysis, instead of models proposed by Beverton and Holt (1957), and others.

Schaaf and Huntsman (1972) presented a Ricker spawner-recruit curve for Atlantic menhaden. The same catch data and basically the same methodology were used in this study, with one important modification. Instead of using the estimated total number of spawning age fish as the independent variable to estimate recruitment, the potential number of eggs that could be produced from the spawning stock was used. This annual potential is influenced by the age distribution of the spawners and their average size. The potential number of eggs produced each year and at each age (Table 2) was calculated from the estimated number of age 3 and older females (1955-70), their back-calculated length, and the following fecundity relation from data presented by Higham and Nicholson (1964):

$$\ln(E) = 0.3149 + 0.0176(l)$$

where E = thousands of eggs produced per female at length, and
l = back-calculated length at age of annulus formation for age-3 and older fish.

Another deviation from the data used on the original Ricker spawner-recruit curve by Schaaf and Huntsman (1972) is the calculated number of recruits in the 1955-70 year classes. The numbers differ between the two studies because: 1) some adult menhaden were reaged following the initial study which brought about slight changes in estimates of year-class size, 2) the maximum instantaneous fishing mortality rates were averaged for age-specific exploitation rates for age 2-5 fish and were not weighted for numbers at age as was done in the earlier study, and 3) the exploitation rate of age-1 fish was estimated each year based on the exploitation rate of age 2-5 fish instead of an estimated exploitation rate of two-thirds that of older fish as was done in the previous study. This was necessary because shifts in fishing area and effort in recent years have increased the vulnerability of age-1 fish.

The parameters of the Ricker model were estimated from a linear regression of $\ln(R/S)$ on S. Fitting the model (Figure 2) yielded an estimate of S_m equal to 60×10^{12} eggs. This is equivalent to 531 million spawning females spread over ages 3-6, and would produce an average recruitment of 3.68 billion fish at age 1.

TABLE 2.—Estimated number of eggs produced by spawning stock of Atlantic menhaden for each year class by age, 1955-70.

Year	Age 3	4	5	6	7	8+	Total
	Number of eggs $\times 10^{12}$						
1955	36.2	72.1	12.6	4.3	0.9	0.3	126.4
1956	45.7	11.1	52.8	12.5	3.4	1.1	126.6
1957	15.5	15.1	12.2	13.8	1.8	0.6	59.0
1958	11.4	6.3	6.8	4.9	3.0	0.3	32.7
1959	49.0	10.8	5.0	6.0	2.5	1.1	74.4
1960	18.1	36.8	12.6	4.7	1.7	0.5	74.4
1961	146.2	5.5	12.0	1.4	0.6	0.2	165.9
1962	23.9	56.7	7.2	6.4	0.9	0.2	95.3
1963	15.4	8.8	12.2	3.3	1.1	0.2	41.0
1964	8.5	3.8	1.9	2.1	0.5	0.1	16.9
1965	7.8	1.7	0.3	0.4	0.2	+	10.4
1966	3.9	0.9	0.1	+	0.1	+	5.0
1967	9.7	1.0	0.1	+			10.8
1968	6.7	2.0	0.2	+			8.9
1969	9.4	1.4	0.1	+			10.9
1970	7.7	2.9	0.2				10.8

+ = less than 0.05×10^{12}.

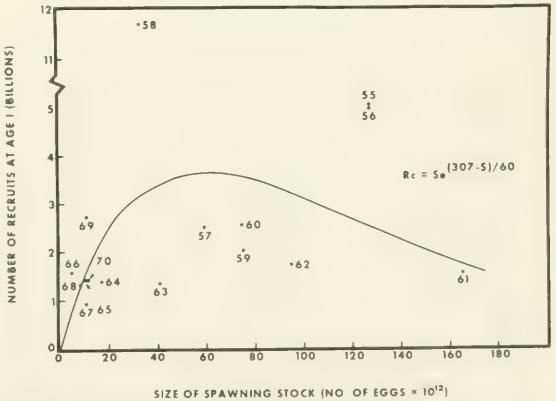

FIGURE 2.—Ricker spawner-recruit relationship for Atlantic menhaden, 1955-70.

Because the regression of $\ln(R/S)$ on S, as is done for the Ricker equation, will automatically give a significant correlation coefficient, a nonlinear fitting procedure was also applied to the data (Marquardt 1963). A comparison of the residual mean squares of the two procedures yielded an F of 1.02, indicating no significant difference in the fit of the Ricker curve to the spawner-recruit data between the standard technique and the nonlinear estimation.

Few published stock-recruitment curves appear to fit the observed data well, and the one for Atlantic menhaden is no exception. Application of a power function of the form $R = aS^b$ to the data resulted in a fit that was not significantly better from that of the Ricker function. The purpose of the study, however, is to examine and explain the deviations from the curve caused by density-independent factors, to see if they can be predicted, and consequently to improve upon a management plan based solely on a long-term, average MSY concept. The survival index (Table 3) represents the ratio of observed recruits (the number of age 1's in the population as estimated from the catch of age 1's and estimated exploitation rates) to the number calculated from the Ricker spawner-recruit model. This ratio is an index of survival, independent of density, and should reflect those environmental effects which influence survival of menhaden from the time of spawning until the time of recruitment to the fishery at age 1.

INFLUENCE OF EKMAN TRANSPORT AND OTHER FACTORS

The influence of transport processes in the southern part of the spawning range is indicated in Figure 3 which depicts the Ekman transport index for the January-March spawning period for 1955-70 and the estimated number of menhaden recruits at age 1 from the year class. The responsiveness of survival to transport shows up well in the Figure where years of strong westward transport correspond with large year classes, and weak transport years with smaller year-class size. Also, increases and decreases in recruitment from one year to the next generally coincide with an increase or decrease in westward transport in the year in which the year class was produced.

The correspondence is weaker in the 1968-70 year classes, although it follows the general pattern. Intense fishing pressure over a number of years changed the age structure of the spawning

TABLE 3.—Estimated number of eggs, observed and expected number of recruits at age 1, and density-independent survival index for Atlantic menhaden, 1955-70.

Year class	No. of eggs $\times 10^{12}$	No. of observed recruits (R_O) $\times 10^6$	No. of expected recruits (R_C) $\times 10^6$	Survival index R_O/R_C
1955	126.4	5,019	2,569	1.95
1956	126.6	4,984	2,568	1.94
1957	56.0	2,538	3,688	0.69
1958	32.7	11,540	3,166	3.64
1959	74.4	2,007	3,599	0.56
1960	74.4	2,568	3,598	0.71
1961	165.9	1,553	1,751	0.89
1962	95.3	1,740	3,253	0.54
1963	41.0	1,378	3,457	0.40
1964	16.9	1,408	2,134	0.66
1965	10.4	1,406	1,472	0.96
1966	5.0	1,579	773	2.04
1967	10.8	922	1,505	0.61
1968	8.9	1,324	1,282	1.03
1969	10.9	2,763	1,521	1.82
1970	10.8	1,415	1,499	0.94

stocks to a considerable extent. For example, approximately 40% of the estimated spawning stock in 1958 were 4 yr or older. The number of age 4 and older fish in the 1969 spawning population was only about 9%, and the average number of eggs per spawning female was about 50,000 less than in 1958. Thus, fishing pressure brought about an even greater reduction in spawning potential than is apparent when considering the number of spawners alone, because of a reduction in the average age. This reduction in real spawning potential reduced the opportunity for a large-scale response to favorable transport in the 1968-70 year classes.

Comparison of the density-independent survival index with Ekman transport yields a surprisingly consistent relationship (Figure 4). A

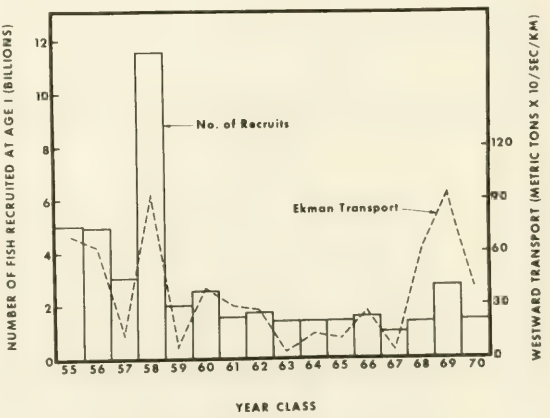

FIGURE 3.—Observed number of Atlantic menhaden recruits at age 1 and sum of average monthly zonal Ekman transport at lat. 35°N, long. 75°W for January-March of spawning years, 1955-70.

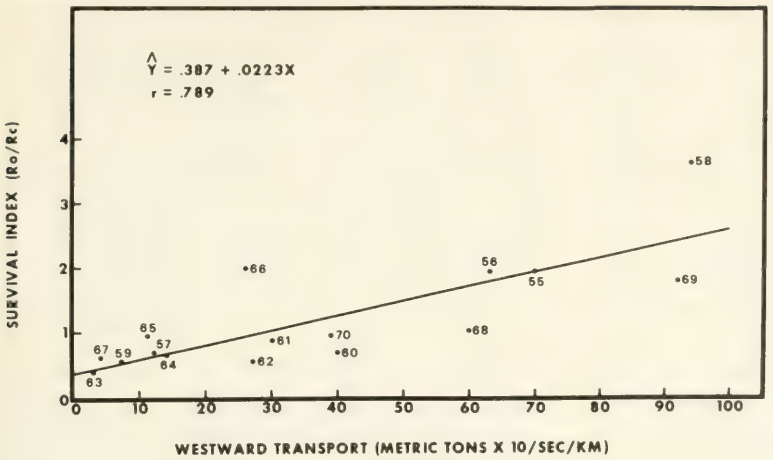

FIGURE 4.—Linear regression of calculated survival index (observed recruits/calculated recruits) for Atlantic menhaden on sum of January-March zonal Ekman transport at lat. 35°N, long. 75°W, 1955-70.

linear regression of survival indices against transport values for the January-March spawning periods at lat. 35°00′N and long. 75°00′W results in an r of 0.789 significant at the 0.001 level with 14 df (Figure 4). This accounts for approximately 62% ($r^2 = 0.622$) of the variation between observed and expected recruitment. Since the transport is indicative of conditions over only a portion of the total spawning range of Atlantic menhaden, and since r^2 accounts for such a large share of the total variation in overall recruitment, the actual effect of transport processes in the southern spawning area must be of overriding significance for the survival of spawn south of Cape Hatteras. With the exception of 1966, the index of survival was greater than 1.0 only when the Ekman transport index indicated a strong westward transport for the January-March period of menhaden spawning activities south of Cape Hatteras.

The transport data fall conveniently into groups of 0-200, 200-500, and 500-1,000 metric tons/s·km of ocean front. Five years of strong westward transport (>500) were found, and in all of these years the survival index was greater then 1.0. The observed recruitment exceeded the expected by an average of 108%, with the 1958 year class showing the largest value. In 6 yr of low westward transport (0-200), the survival index was never greater than 1.0. In 5 yr of moderate or "average" westward transport, (200-500) high survival occurred in 1 yr, and poor or moderate survival in the other 4 yr, indicating the influence of additional factors over the spawning range that are operating to produce variations in year-class strength. The high index for 1966 may partially result from the fact that the estimated spawning stock production of 5×10^{12} eggs was, by far, the lowest of any year on record (Table 2). Under such low stock size, density-dependent survival may have exceeded that indicated by the Ricker curve, creating an artificially high index of survival. A slight underestimation in the computation of the number of spawners would also create a very high survival index, since the slope of the Ricker curve is extremely steep as spawning stock size approaches zero (Figure 2).

Transport values at lat. 33°N, long. 78°W, approximately 200 nautical miles southwest of lat. 35°N, long. 75°W were also considered. The data are from a point offshore of Long Bay, S.C., the southernmost of the cuspate Carolina bays, and serves as an indicator of Ekman transport in the extreme southern part of the Atlantic menhaden spawning range. A significant correlation existed between transport for the January-March period and the survival index (Table 4). Due to the correlation between the two transport values south of Cape Hatteras, however, little additional variation is accounted for by the southernmost transport value (Table 5). Since transport is a function of wind stress and Coriolis force, movements of air masses through the southeastern United States would give parallel transport values at the two locations, with intensity of transport dependent on variations within the air mass. The large amount of variation accounted for by the two transport indices south of Cape Hatteras is sufficient to account for the relative success or failure of a year class, and supports the observation that a significant portion of menhaden spawning takes place south of Cape Hatteras.

TABLE 4.—Stepwise regression of survival index of Atlantic menhaden on environmental factors.

Factor	No.	Time of year	Correlation with survival index	individual level of significance	Cumulative correlation	Error mean square	Cumulative percent of variance
Zonal Ekman transport lat. 35°N, long. 75°W	X_1	Jan.-Mar.	0.789	0.001	0.789	0.298	62.2
Chesapeake Bay discharge	X_6	July-Sept.	−0.216	—	0.825	0.271	68.0
Zonal Ekman transport lat. 39°N, long. 72°W	X_3	Nov.-Feb.	0.352	—	0.840	0.270	70.6
Zonal Ekman transport lat. 39°N, long. 75°W	X_4	Nov.-Feb.	0.519	0.05	0.896	0.198	80.3
Minimum temp Delaware Bay entrance	X_5	Jan.-Feb.	−0.177	—	0.914	0.181	83.6
Zonal Ekman transport lat. 33°N, long. 78°W	X_2	Jan.-Mar.	0.720	0.005	0.919	0.190	84.5

TABLE 5.—Regression coefficients between independent environmental variables used in the recruit-environment predictive equation for Atlantic menhaden. See description of X's in Table 4.

	X_2	X_3	X_4	X_5	X_6
X_1	0.789	0.645	0.644	−0.333	0.032
X_2		0.589	0.701	−0.580	−0.068
X_3			0.868	−0.403	0.174
X_4				−0.510	0.213
X_5					0.023

Wind-driven transport off Delaware Bay was studied as being representative of menhaden spawning areas in the Middle Atlantic Bight. Because the transport values are produced in a 3° grid by the Pacific Environmental Group, there were no available data for a point located centrally on the continental shelf. Two locations were chosen: one at lat. 39°N, long. 75°W, near the mouth of Delaware Bay, the other at lat. 39°N, long. 72°W, near the outer edge of the continental shelf. The two locations are approximately 260 km apart in an east-west direction, and are felt to be representative of Ekman transport over the broad shelf area near the east-west axis of the Middle Atlantic Bight.

The entrance of larvae into estuaries of the Middle Atlantic Bight occurs variably from September to June, with peak immigration occurring in the winter. Reintjes and Pacheco (1966) reported on 6 yr of larval collection at Indian River, Del., and showed high rates of influx from December through March. The peak month varied from year to year, but stayed within the December-March period. Correlation coefficients between summed transport values for November-February (the peak period of larval drift) and the survival index (Table 4) are not as large as those from south of Cape Hatteras, but the effect of transport on survival at the inshore point (lat. 39°N, long. 75°W) is significant at the 0.05 level. The transport values from the inshore and offshore points account for approximately 27% and 12%, respectively, of the total variance in the survival index for Atlantic menhaden. When combined with the transports south of Cape Hatteras, these values for the Middle Atlantic Bight account for an additional 12+% of the residual variance. Correlation coefficients are lower than those found for the South Atlantic Bight, and may be indicative of: 1) major nearshore spawning activities, reducing the need for a suitable transport mechanism; 2) a lower level of spawning in the area; or 3) a lower level of recruits per spawner due to mortalities from other environmental factors in the area.

The model of circulation off Chesapeake Bay developed by Harrison et al. (1967) and discussed in the Larval Transport section would be appropriate if larval menhaden were demersal in nature. However, since larvae are more abundant in the upper water column, we would expect a negative relationship between discharge and survival in the Middle Atlantic Bight because high surface discharge would impede larval entrance into estuaries. Chesapeake Bay was chosen to test that hypothesis because of its importance as a major nursery area. Average monthly discharge rates from the Susquehanna, Potomac, and James rivers were used in the test because they constitute over 90% of the total inflow into Chesapeake Bay. Discharge during the third quarter (July-September) of the year preceding the year-class year was chosen because there is a lag time of up to 90 days between stream flow and bay discharge (Harrison et al. 1967). The influence from run-off would be felt at the mouth of the Bay in the October-December period when larvae begin entering in increasing abundance. A correlation between the survival index and discharge rate did not result in a significant

coefficient (Table 4). When combined with the other factors considered above, Chesapeake Bay discharge accounts for an additional 6% of the residual variance in density-independent year-class strength. A fairer test of the effects of discharge on larval transport would require that we isolate that portion of the total larval production that would enter Chesapeake Bay under varying conditions. Our knowledge of Atlantic menhaden spawning activities is not sufficient to do this with reasonable precision.

An absence or reduction in the number of larvae in estuaries during periods of extreme cold has been noted by June and Chamberlin (1959) and Reintjes and Pacheco (1966). Kendall and Reintjes (1975) hypothesized that severe winters, particularly in the northern segment of the spawning range, result in heavy kills of overwintering larvae in the estuaries. In addition, laboratory acclimation studies have shown high mortality rates when menhaden larvae were held for several days at temperatures below 3°C (Lewis 1965). A time series of minimum mean monthly sea surface temperatures was located for the mouth of Delaware Bay from National Ocean Survey Tide Station Observer Records (U.S. Department of Commerce 1973). These data were considered representative of mid-to-northern coastal areas in the Middle Atlantic Bight. Correlation of the survival index for the entire population and the minimum temperature yielded a low correlation coefficient (Table 4). The correlation is somewhat of an artifact, however, and probably is biased by the positive correlation between Ekman transport and year-class strength. Westward Ekman transport is generated by winds from the north. Years of high westward transport in winter months are years of sustained north winds, which are associated with cold air masses. Under such conditions, we would expect cooler sea-surface temperatures in those years, particularly in or near shallow estuarine areas. There may be a positive correlation between temperature and survival, but the relationship probably is masked by the overriding effects of wind-generated Ekman transport (Table 5). The low correlation coefficient could also indicate that only a small portion of the population would overwinter in northern waters where temperature stress might be a significant factor.

If low temperature reduces survival, a transport mechanism to carry fall-spawned larvae southward along the Middle Atlantic Bight into the vicinity of estuaries that have milder winter temperatures would be a positive survival factor. Therefore, the meridional (north-south) component of Ekman transport in the Middle Atlantic Bight at lat. 39°N, long. 72°W near the edge of the shelf off Delaware Bay was considered. A correlation between the survival index and the southward transport for the October-December spawning period resulted in a coefficient of 0.336, which accounts for about 10% of the total variance in density-independent recruitment. However, the contribution to reduction in residual variance was minimal, because all of the variation due to southward transport was accounted for by linearly related east-west zonal Ekman components already considered. A relatively steady state southward transport mechanism exists in the Middle Atlantic Bight in the form of a southward flowing current over the shelf (Bumpus 1973). Because this current is quasi-permanent, variations in southward Ekman transport may be of little significance and may only create minor fluctuations in strength of an existing transport mechanism.

RECRUIT-ENVIRONMENTAL MODEL

The logic used in the selection of environmental parameters for inclusion in a model of environmental effects is depicted schematically in Figure 5. The heavy line represents an intuitive weight of density-dependent and density-independent factors in the survival of menhaden larvae from the time of spawning through their oceanic phase. In the upper Middle Atlantic Bight, for example, spawning takes place close to shore or in major bays and sounds, reducing or eliminating the time spent by larvae in the open ocean. This would reduce dependence on favorable currents for transport. Under such conditions, environmental factors influencing mortality may be relatively stable, with variation in the number of fish spawning in the area being the probable cause of most of the variation in the number of recruits produced. In the South Atlantic Bight, however, spawning takes place offshore, and dependence on favorable ocean currents would seem to have greater weight than spawning stock size on survival. Large annual variations in transport would produce large variations in survival in the South Atlantic Bight at a given stock size. The lower Middle Atlantic Bight seems to be an intergrade between the two extremes, with sig-

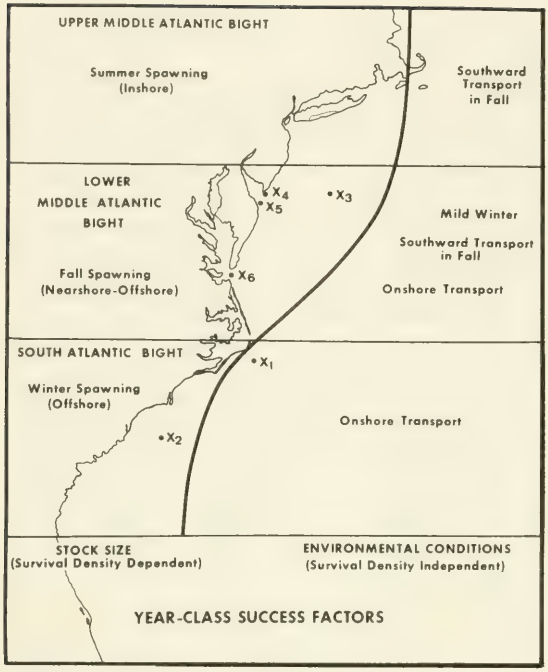

FIGURE 5.—Schematic representation of logic used in the development of the survival index predictive model. Location of environmental parameters used in the model is indicated by Xn, description of parameters in Table 4.

nificant spawning taking place farther offshore as adults migrate southward in the fall. This should result in increased significance of oceanic transport factors from north to south in the determination of year-class strength. The hypothesis of increasing importance of transport as spawning activities move progressively farther offshore is supported by the highly significant correlations between the survival index and transport values south of Cape Hatteras and similar correlations which have a lower level of significance off Delaware Bay.

The selection of locations and time periods for Ekman transport data was based on the availability of data for specific coordinates, desire for representation of broad spawning areas, and estimates of larval drift time and direction (Figure 5). Of the many possible environmental factors which could influence survival during the oceanic phase, three (transport, temperature, and river discharge) were chosen because they appeared to be factors of major importance and data series were available for the same period in which vital statistics of the Atlantic menhaden populations have been taken.

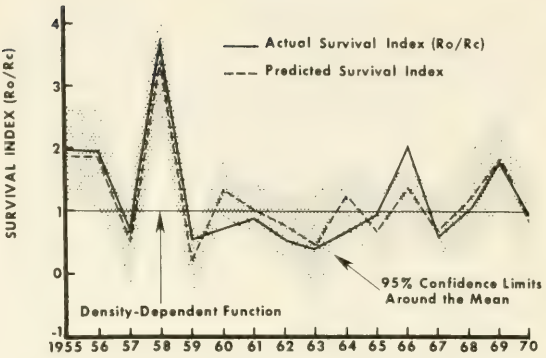

FIGURE 6.—Multiple regression of the survival index for Atlantic menhaden on environmental factors, 1955-70. Predictive equation and listing of environmental factors presented in text. Correlation coefficients and model data presented in Tables 4 and 6.

TABLE 6.—Data used in recruit-environment predictive model for Atlantic menhaden. Location of factors identified in Figure 5, individual factors identified in Table 4.

Year class	S.I.	Environmental factors					
		X_1	X_2	X_3	X_4	X_5	X_6
1955	1.95	70	74	272	152	2.4	9
1956	1.94	64	107	307	271	1.0	30
1957	0.69	12	13	83	34	3.4	29
1958	3.64	94	124	141	169	0.6	9
1959	0.56	7	13	126	82	1.5	24
1960	0.71	40	42	121	78	1.6	11
1961	0.89	30	33	155	129	1.6	22
1962	0.54	27	63	149	79	1.4	17
1963	0.40	3	70	206	158	−0.3	9
1964	0.66	14	43	120	127	2.0	16
1965	0.96	11	32	96	35	1.8	7
1966	2.04	26	55	125	104	1.3	7
1967	0.61	4	21	98	63	1.8	8
1968	1.03	60	96	161	97	0.0	23
1969	1.82	92	76	317	212	0.4	16
1970	0.94	39	47	185	156	0.2	28

The multiple-regression model developed to relate recruitment to environmental variables yields a correlation coefficient of 0.919, significant at 0.003 with 9 df (Figure 6). Model data are given in Table 6. The model accounts for over 84% of the variance in the actual survival indices (Table 4). Translated into recruits, the model indicates that over 84% of the variation between actual recruitment into the fishery and expected recruitment during the 1955-70 period is accounted for by environmental fluctuation. The model is described by the equation:

$$S.I. = 0.4148 + 0.0205X_1 + 0.00530X_2 - 0.00807X_3 + 0.00950X_4 + 0.23967X_5 - 0.02679X_6 \pm e$$

where $S.I.$ = survival index computed by dividing observed recruits by expected recruits

X_1 = sum of monthly average zonal (westward) Ekman transport rates for January-March of the year-class year at lat. 35°N long. 75°W

X_2 = sum of monthly average zonal (westward) Ekman transport rates for January-March of the year-class year at lat. 33°N, long. 78°W

X_3 = sum of monthly average zonal (westward) Ekman transport rates for November-December of the year prior to the year class and January-February of the year-class year at lat. 39°N, long. 72°W

X_4 = sum of monthly average zonal (westward) Ekman transport rates for November-December of the year prior to the year class and January-February of the year-class year at lat. 39°N, long. 75°W

X_5 = minimum mean sea surface temperature at the mouth of Delaware Bay in the year-class year

X_6 = sum of monthly average discharge rates from Susquehanna, Potomac, and James rivers in July-September of the year preceding the year-class year

e = error term.

The predicted number of recruits for each year is given by:

$$R_p = R_{ci} \times S.I.$$

where R_p = predicted number of recruits

R_{ci} = number of recruits calculated from the Ricker curve at spawning stock size in the ith year.

A correlation between the observed number of recruits (R_o) and the predicted recruits (R_p) for each year yields a coefficient of 0.943 and a slope of 0.914 with no systematic bias around the regression line. Further evidence of the validity of the model is the failure of adjustments to increase the percent of variance accounted for by the environmental factors. The initial model, based on judgments of the proper time and location of environmental parameters, yielded a higher correlation coefficient than any subsequent models in which any of the parameters or time-spans were varied away from those which were considered the most significant from a biological standpoint. The parameters were not selected by a screening process from a large number of variables, but were selected because of their probable impact on survival.

The four largest year classes (1955, 1956, 1958, and 1969) during the 16-yr period are accurately described by the model. The average error of prediction for these years is 4.3% and the maximum error is 6.3%. Smaller year classes are not described with the same degree of accuracy, although the mean error for the 16-yr period is reduced from 1.5 billion fish using only the Ricker curve to 610 million individuals per year by the model, and the standard error of the mean is reduced from 501 to 155 million fish.

The multiple-regression model has a high correlation coefficient and therefore describes the data well. Its value for prediction is somewhat more tenuous and requires testing on a subsequent set of data to determine its accuracy. The model was not broken into separate time-series units for testing because of the brevity of the 16-yr data base.

The model is a first-cut approximation for the evaluation of transport and other factors. The number of variables included tends to increase the R^2 value, even though some parameters do not show individual significance levels when correlated with the survival index. However, only the Chesapeake Bay discharge has a β value of which ± 2 standard errors encompasses 0, indicating that the factor is probably not significant. The other parameters are associated with the same major air mass movements, and are therefore interrelated. A more sophisticated model should be based on either principal components regression or Ridge regression techniques to correct for the interdependence of some of the parameters and to improve the predictive capability. A reduction in the number of variables used is desirable from a statistical standpoint because of the short time span of the data base. Regression of the survival indices on the three transport values off of Cape Hatteras (lat. 35°N, long. 75°W) and Delaware Bay (lat. 39°N, long. 72°W; lat. 39°N, long. 75°W) yields an R^2 of 0.741 (12 df, $P<0.001$). The abbreviated model accounts for a significant portion of the variance around the spawner-recruit curve. It describes the data for high and low survival years nearly as well as the full model and probably has a similar predictive capability. Determination of the actual influence of the other factors (dis-

charge and temperature) which were included because of their potential biological importance will require a greater knowledge of spawning intensities and a longer term data base.

Overall, the model implies a predictive capability for large year classes and for extremely poor year classes. The model provides a satisfactory indication of the general magnitude of a year class prior to entering the fishery in 14 of the 16 yr.

For initial model purposes, the survival index was not computed beyond 1970 because the 1971 year class is still being harvested by the fishery, and the total catch from that year class necessary for verification of the number of recruits is not known. Forecasting in real time can be accomplished by inserting the routinely available environmental data into the survival index equation. The expected number of recruits for a given year class is obtained by determining age structure and abundance of 2-yr-old and older fish from fishery landings the previous fishing season, estimating an exploitation and survival rate to determine the number that will survive to spawn the next year class, calculating the expected number of eggs produced, and estimating the expected number of recruits from the Ricker function. Multiplying the expected number of recruits by the predicted survival index gives the predicted number of recruits. Estimates of the number of recruits can be made as early as April of the year-class year, and can be revised when actual exploitation rates are determined to allow better estimates of the size of the spawning stock which produces the year class. Thus, an initial prediction of the number of recruits can be made approximately 1 yr before they become available to the fishery the following spring.

DISCUSSION

Refinement of the predictive capability of the recruit-environment model is dependent on increased knowledge of the biology of Atlantic menhaden and on better understanding of the effects of the many factors that influence distribution, abundance, and survival. The model is concerned only with variation introduced into year-class size during the relatively short life phase in which larvae are oceanic and before metamorphosis takes place. The model concentrates on those factors which influence larval distribution and act as a mechanism to transport larvae into the vicinity of estuarine nursery grounds, thereby increasing survival. Major sources of variation such as food availability and predation have not been directly considered. However, since these factors are, to some extent, influenced by the number of larvae produced by the spawning stock, variations induced by them should be partially accounted for by the density-dependent Ricker function. The actual fluctuation in availability of food could only be determined by broad-scale surveys over the entire menhaden spawning range and would require a continuous time series for a number of years. Likewise, the determination of predation and cannibalistic influences would require extensive field surveys and controlled laboratory experiments.

Problems in determining the influence of pertinent environmental factors are compounded by the large geographic range of menhaden spawning activities. The influence of any one particular factor at a specific location could only be determined if the amount of spawning at that location was known. Comparison of environmental factors against a survival index for the entire stock, as has been done in this study, requires the selection of broad-scale factors having major influence over large portions of the spawning range, or the selection of representative data which provide a generalized environmental index for a selected factor. Localized variations may be highly significant, but masked by overall survival success or failure without knowledge of localized spawning intensity.

Cushing (1969, 1974) cited failures in attempts by other authors to correlate year-class strength and winds (or pressure gradients), and suggested that variation in wind direction may be a greater source of variation than the strength of winds from a single direction. The U.S. east coast is composed of an almost continuous series of bays and sounds, which extend both north and south of the major spawning region for Atlantic menhaden. Under these circumstances, variations in wind direction would probably influence the route of larval drift. However, unless northward or southward larval movement was extreme, larvae would not be transported away from suitable nursery areas as long as there was a significant onshore component of wind-driven circulation. Thus wind direction would be a significant factor only if that direction reduced the westward component of Ekman transport or if the normal seasonal wind pattern reversed, generating eastward (offshore) transport.

Comparison with Pacific Sardine

Computed survival indices allow comparisons between the Pacific sardine and Atlantic menhaden, in addition to those detailed by McHugh (1969). Radovich (1962) presented data for Pacific sardine showing the effect of good, average, and poor environmental conditions on the spawner-recruit relationship. He used maximum and minimum parabolas based on highest and lowest recruitment years and identified the area between the curves as indicative of the effects of the environment as well as spawning stock size on recruitment. A similar approach, modified by using the right-hand skewed Ricker curve yields similar results (Figure 7). Year classes used in the computation of the maximum and minimum recruitment curves for Atlantic menhaden were not selected for high and low recruitment as was done by Radovich, but were selected because they represented extremes in the variation of transport factors. The maximum recruitment curve was developed from year-class size during the 3 yr of highest ($\geq$700 metric tons/s·km) southern onshore transport (1955, 1958, 1969). Similarly, the minimum recruitment curve was computed from year-class size during the 3 yr of lowest ($<$100 metric tons/s·km) onshore transport (1959, 1963, 1967). The two curves represent a wide range of environmentally induced fluctuation around the stock and recruitment curve calculated from the 1955-70 data base. No statistical significance can be attached to the upper and lower curves because each is based on three data points. However, the figure indicates the range of variance that masks the density-dependent function if pertinent environmental factors are not identified and weighted for effect at various stock sizes. The greater slope of the maximum curve is of particular interest, indicating a significant loss of potential recruits in good environmental years if adequate stock size is not maintained.

Additional parallels can be drawn between Pacific sardine and Atlantic menhaden spawner-recruit relationships during periods of overfishing and low survival. A comparison of spawning stock size and year-class size for the two species linked in chronological order shows striking similarities (Figure 8). In each case, there was a period of several years at high stock size in which the size appeared to be near or past the maximum needed to produce large numbers of recruits. A series of

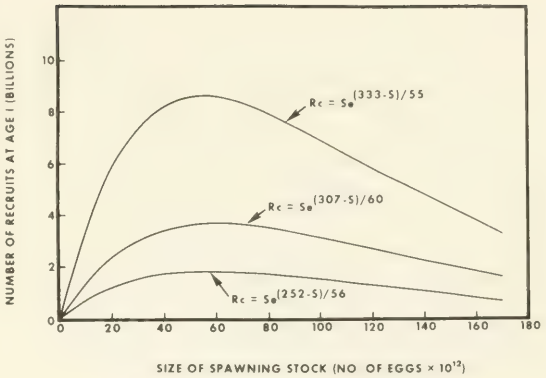

FIGURE 7.—Ricker spawner-recruit relationships calculated for years of good and poor environmental conditions. The upper curve is calculated from observed recruitment during the three greater years of Ekman transport, the middle curve is calculated from the 16-yr data set, and the lower curve is calculated from observed recruitment during the three lesser years of Ekman transport.

good year classes (1937-39 for sardine; 1955, 1956, and 1958 for menhaden) was followed by a series of poor survival years (1940-45 for sardine, 1959-64 for menhaden). These reductions in recruitment, combined with excessive fishing pressure, reduced spawning stock size drastically, leading to a restabilization of stock and recruitment around small stock levels. In the case of menhaden, the 5-yr period of decline reduced the spawning stock size by an order of magnitude. By 1966, spawning potential had dropped to a low of 5×10^{12} eggs from the 1961 high of 165×10^{12}. The parallel between the two sets of data is a cause for concern, because the decline and apparent restabilization of Pacific sardine stocks was followed by a complete collapse of the fishery. Henry (1971:23) in his analysis of the decline of the Atlantic menhaden fishery stated, "I am concerned that the stocks of Atlantic menhaden may have been reduced to a level that is having an adverse effect on recruitment." Clark (1974:14), in a study of the effects of schooling on population dynamics on small schooling species (as in the case with Atlantic menhaden), concluded that, "A commercial fishery based on such a species might be expected to experience a rather spectacular population collapse, which could be brought on either as a direct result of an increased fishing effort which suddenly transforms the system into an unstable mode, or as an indirect result of fishing which reduces resiliency and renders the population vulnerable to the effects of random environmental fluctuations." The possibility of a complete collapse in the Atlantic

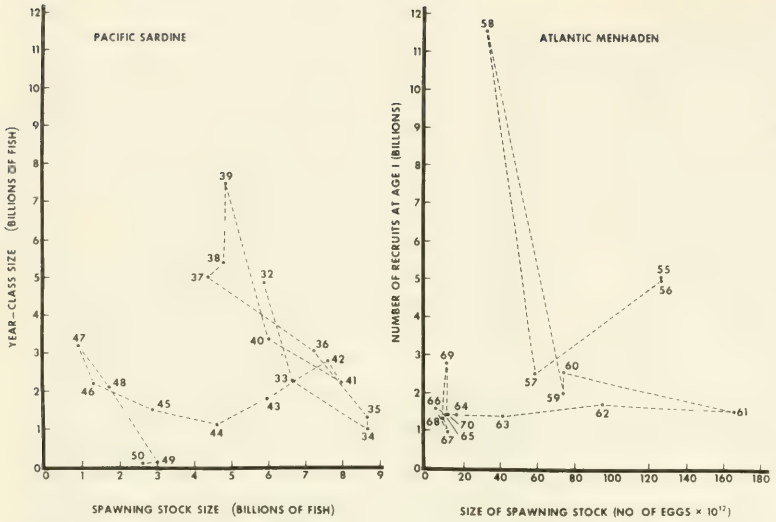

FIGURE 8.—Year-class size related to spawning stock size and linked in chronological order for Atlantic menhaden and Pacific sardine. Pacific sardine figure after Radovich (1962:134).

menhaden fishery, given high fishing effort and additional years of poor survival, cannot be discounted.

Fortunately, there are significant differences in the environment, biology, and fishery of Pacific sardine and Atlantic menhaden. One of the more important differences is the estuarine dependence of menhaden. In every year, at least some estuarine systems on the east coast should provide favorable environments, insuring good survival of larvae which reach those nursery grounds. Also, spawning activities spread over the entire coast should include at least some areas conducive to survival, reducing the chance of almost no survival over the entire range. Climatic change which shifts the distribution of menhaden spawning activities would not likely shift the spawning region far enough away from suitable nursery areas to cause the type of massive failure that occurred in the sardine fishery. Another significant factor in the collapse of the sardine stocks was an increase in the stock size of competing species, filling the niche in the ecosystem as the sardine population decreased. Although there is no fishery for species which are potentially competitive with Atlantic menhaden and adequate stock data on such species are not available, there are no indications of large increases in abundance of any coastal pelagic species, and the niche available to menhaden appears to be open. However, John Radovich (pers. commun., California Department of Fish and Game) points out that "the value of not having identified an increase in competitors for the menhaden may be of little significance because:

1) The sardine collapse and failure to recover may have happened without a 'competing' species such as the anchovy.
2) Available forage and habitat may be utilized through slight increases in the abundance of several species, and hence go unnoticed.
3) The capacity within a trophic level may vary considerably so that actual changes in the abundance of competing species may be masked by changes in available forage and habitat."

The menhaden fishery is somewhat self-regulating, in that low stock levels have brought about economic conditions which forced a reduction in effort and closure of processing plants. The closure of plants in the northeast United States during the late 1960's reduced fishing effort on older age-groups, halting the drastic decline in spawning stock size (Schaaf in press). This action, plus good survival in 1966 which produced the spawning stock for the high transport, large year-class year of 1969, is probably responsible for the brief resurgence of the fishery in the early 1970's.

Implications for the Fishery

Implications for the fishery are rather straightforward: in years of poor environmental conditions recruitment is low regardless of stock size; extremely low spawning stock sizes in years of poor environmental conditions result in recruitment below the level needed to maintain the fishery; favorable environmental years will

produce exceptional year classes and a proportionally greater harvestable surplus at stock sizes near the spawning optimum; and a series of poor environmental years (1959-64), coupled with excessive fishing pressure, will reduce stock size to a level which produces little harvestable surplus.

During the 16 yr covered by this study extremely large year classes were produced in 3 yr (1955, 1956, and 1958). Favorable conditions in 1969 resulted in a high survival rate, but only produced 2.7 billion recruits because of small spawning stock size. In one other year (1966) survival occurred that was greater than expected, but at extremely low stock size. In the other 11 yr recruitment was either near, or well below the expected level, compounding the stock depletion caused by excessive fishing pressure. The drastic reduction in stock size resulted in a restabilization of the stock-recruitment relationship around a low stock level. This is evidenced by the steady decline in catches from 1956 to a low of 162,000 metric tons in 1969, followed by slightly higher catches in succeeding years (Table 7). Extremely large catches in the late 1950's are the result of the unusual coincidence of 3 high survival years within a 4-yr span. Average survival over the 16-yr period was much lower, and average year-class size would be considerably smaller, even at optimum spawning stock size.

Schaaf and Huntsman (1972) gave MSY estimates for Atlantic menhaden of 600,000 metric tons based on an equilibrium catch-effort curve from historic data and 380,000 metric tons from a population-prediction model. The population-prediction model dampens the effects of large year classes and probably comes closer to representing long-term MSY than the higher estimates.

The maintenance of optimum spawning stock size and several year classes in the spawning stock is vital to insure adequate response to favorable environmental conditions. Based on the estimated survival rates over the 16-yr period, and the optimum spawning stock size from the Ricker function, surplus yield was calculated under conditions which would maintain four spawning groups (ages 3-6) in the populations. The calculation of surplus yield is based on an instantaneous natural mortality of 0.42 and fishing mortality of 0.36 spread over 6 yr within a year class (ages 1-6) and assuming that one-half of the age-1 recruits are vulnerable to the fishery. A full complement of years 1-6, from year-class data available after 1954, was not obtainable until 1961, when 6-yr-old fish were harvested from the 1955 year class. Under the conditions imposed on the harvest, the allowable catch, computed for 1961-71, averaged 419,000 metric tons/yr (Table 7). Extremes in the allowable catch would have ranged fron 227,000 to 633,000 metric tons, depending on the size of year classes which constituted stock size in a particular year. This catch is similar to the MSY estimates of Schaaf and Huntsman (1972), and was computed for a period in which most of the year classes had less-than-expected survival. The survival index was well below 1.0 from 1959 to 1964, a period of six continuous years, and is reflected by the decline in surplus stock during that period. Actual catches made by the fishery from 1955 to 1971 (Table 7) averaged approximately the same as MSY, but

TABLE 7.—Catch of Atlantic menhaden at MSY for actual survival rates, 1955-70 year classes, fishery landings, 1955-71, and predicted surplus from recruit-environment model.

Year of harvest	Potential catch at S_m			Actual catch by fishery			Predicted catch
	No.in billions	Wt (thousand metric tons)	Wt/fish (g)	No.in billions	Wt (thousand metric tons)	Wt/fish (g)	Wt (thousand metric tons)
1955				3.12	641.4	206	
1956				3.56	721.1	203	
1957				3.51	602.8	172	
1958				2.72	510.0	188	
1959				5.35	659.1	123	
1960				2.78	529.8	191	
1961	1.68	632.9	377	2.60	575.9	222	510.9
1962	1.38	488.1	354	2.01	537.7	268	466.7
1963	1.10	410.0	373	1.76	346.9	197	412.5
1964	0.88	339.0	385	1.73	269.2	156	392.5
1965	0.76	226.6	298	1.50	273.4	182	295.5
1966	0.99	254.9	257	1.34	219.6	164	374.2
1967	1.72	367.4	214	0.98	193.5	197	371.5
1968	1.62	472.0	291	1.14	234.8	206	405.1
1969	1.40	426.0	304	0.87	161.6	185	387.0
1970	1.81	464.7	257	1.40	259.3	185	471.5
1971	1.78	525.6	295	0.97	250.3	258	521.6
Mean	1.37	418.8	306	2.20	410.4	178	419.0

were taken by extensive overfishing in the late 1950's and early 1960's, with a resultant decrease in spawning stock size and age structure. The average catch from 1955 to 1963 was 596,000 metric tons, well above the MSY level. The fishery also took greater numbers of fish of smaller size than was compatible with management to insure adequate numbers of spawners. Thus overfishing, which reduced stock size, was compounded by a series of poor environmental years, further reducing the spawning stock to a level below that necessary to provide large surplus yields from the higher survival years of 1966 and 1969. Had optimum spawning stock size been maintained, the fishery should have been able to increase its yield during the 1967-71 fishing seasons by an average of 231,000 metric tons/yr.

The value of a predictive model lies in its usefulness for developing strategies to take advantage of exceptional year classes or to avoid overexploitation of poor year classes. Catches based on the number of recruits calculated from the survival index model are similar to MSY and to those averaged by the fishery (Table 7). However, the absolute mean error from the allowable surplus is approximately 134,000 metric tons/yr for the actual fishery landings (1961-71) and 48,000 metric tons/yr if harvest had been limited to the predicted surplus. Some overfishing would have occurred because of errors in prediction, but it would have been significantly less than that imposed by the fishery during earlier years. Fishing at a level necessary to harvest the predicted surplus would have provided reasonably stable catches, maintained several age-classes in the fishery, maintained adequate spawning stock, and prevented excessive exploitation of the stocks, all desirable factors in the management of fishery resources.

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EFFECTS OF BENZENE (A TOXIC COMPONENT OF PETROLEUM) ON SPAWNING PACIFIC HERRING, *CLUPEA HARENGUS PALLASI*

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ABSTRACT

When female Pacific herring were exposed to low (parts per billion) levels of benzene for 48 h just prior to their spawning, a significant reduction occurred in survival of ovarian eggs and resultant embryos and larvae through yolk absorption. The reduction in survival of ovarian eggs was approximately 10-25%, for embryos from fertilization to hatching, 26%, and for embryos and larvae through yolk absorption, 43%. Exposure to benzene also induced premature spawning and resulted in aberrant swimming behavior and disequilibrium in adults of both sexes.

The maximum accumulation of ^{14}C-labeled benzene and/or metabolites in ovarian eggs (14 times initial concentration in water in 24-48 h; 1.4 μl/g from 0.1 μl/liter) was greater than in later egg and larval stages as measured in other experiments.

Conservatively estimating the total reduction in survival in these experiments to be approximately 50% through yolk absorption, I surmise that the effect of exposing spawning herring to only one toxic component of petroleum could have a significant effect on the population. The fish in these experiments were exposed to relatively high parts per billion levels, but they were exposed for a relatively short period (48 h); it is probable that in the estuary, if chronically exposed over a longer period of time to low parts per billion levels of aromatic components, the populations could be seriously affected.

When the spawning female herring is compared with other life history stages, we find that the spawning stage is clearly the most sensitive of those tested. If fishes prove generally to be most sensitive to petroleum components during their spawning seasons, fishery management decisions should take this factor into consideration in protecting the resources.

In studies of pollutant effects on marine organisms, emphasis should be placed on critical or sensitive life history stages. With this in view, research on petroleum effects on fish has been directed more recently toward egg, embryo, and larval stages (Kühnhold 1969, 1972; Evans and Rice 1974; Struhsaker et al. 1974). Results in many studies revealed that fish egg and larval stages were surprisingly resistant to crude oil and water-soluble and aromatic fractions of crude oil. Some of this resistance in fish is probably attributable to the presence of enzymes for metabolic detoxification of components with ensuing rapid depuration and physiological homeostasis (Lee et al. 1972; Neff 1975; Korn, Hirsch, and Struhsaker 1976, footnote 2).

I have observed, as expected, that the effects of exposure of monoaromatics such as benzene are more severe at all life history stages if fishes are otherwise stressed by environmental extremes or are in poor "condition" from inadequate nutrition. On this basis it is suggested that the female at time of spawning may be the most sensitive stage to toxic oil components. In herring, for example, the fish often feed poorly for some time prior to spawning and have low fat and energy reserves associated with the production of eggs (Blaxter and Holliday 1963). Anadromous fishes or fishes such as herring which migrate into estuaries for spawning may also be exposed to environmental extremes, particularly to changes in salinity, which produce additional stress. Further, since aromatics are highly lipid-soluble, it might be expected that benzene would accumulate to high levels in ovarian eggs. These factors could lead to significant reductions in fecundity and serious consequences for populations over long chronic exposures.

The purpose of this experiment was to examine the effect of benzene on female Pacific herring, *Clupea harengus pallasi* Valenciennes, just prior to spawning. We have also studied benzene effects on other life history stages of the herring (Struhsaker et al. 1974; Korn et al. see footnote 2;

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[2]Korn, S., N. Hirsch, and J. W. Struhsaker. 1976. The uptake, distribution, and depuration of ^{14}C-benzene and ^{14}C-toluene in Pacific herring (*Clupea pallasi*). Unpubl. manuscr.

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Eldridge et al.[3]). So far as we know, there is no similar study, exposing fish just prior to spawning, for any oil component.

Benzene was selected for most of our studies on herring because of its relatively high proportion in the water-soluble fraction of crude oil and refined products (Anderson et al. 1974), high solubility in water and relative toxicity (Benville and Korn 1974, footnote 4; Korn, Struhsaker, and Benville 1976). Monoaromatics were tested individually rather than exposing fishes to the total oil or total water-soluble fraction in order to more specifically delineate physiological responses to a known toxic component.

Initial research on Pacific herring adults, eggs, and larvae was conducted with high (ppm level) concentrations of benzene (Struhsaker et al. 1974; Korn, Struhsaker, and Benville 1976). Because of the high volatility of benzene, such concentrations would probably occur only briefly after catastrophic incidents, such as tanker accidents and well blowouts. Subsequently, we tested levels in the low ppb (parts per billion) range as being more representative of chronic exposures and potentially more damaging over a long period to marine populations.

In this study, ripe male and female herring were exposed just prior to spawning to 100 nl/liter (ppb) and 800 nl/liter (ppb) benzene for 48 h. The ^{14}C-labeled benzene and its metabolites were measured in the ovaries to determine uptake, accumulation, and depuration. Exposure effects on behavior, the mortality of eggs in the gonads of females, and rate of delayed mortality in embryos at hatching and larvae through yolk absorption were also recorded.

METHODS

Pacific herring were captured 4 December 1974 during the spawning season in San Francisco Bay by a local bait dealer. The fish were captured with a lampara net and wet-brailed from the net into the vessel bait wells. The fish were transported immediately in the bait vessel to the Tiburon Laboratory dock and then transferred to 1,900-liter tanks in the laboratory. Fish were "running ripe" when captured. Because the purpose of these experiments was to expose fish prior to spawning, an acclimation period of only 24 h was allowed. Previous experience with ripe herring has shown that they usually spawn shortly after capture.

Fish were initially placed in circular tanks with double sand-filtered, open flow seawater at ambient conditions in the bay at the time. Initial handling mortality was negligible. During the experiment, conditions were as follows: salinity, 23.0-24.0‰; temperature, 10.0°-11.5°C; oxygen, 6.0-10.5 ppm. An ambient benzene concentration was undetectable at the ppb level. Since herring generally feed poorly when spawning, neither exposed nor control fish were fed during the experiment. The exposure treatments were as follows:

Control: 0 nl/liter (ppb) benzene; open flow system, no benzene exposure; approximately 100 fish (50 males, 50 females).

Exposed: 800 nl/liter (ppb) benzene, open flow system, constant exposure for 48 h; approximately 100 fish (50 males, 50 females).

Exposed: 100 nl/liter (ppb) ^{14}C-labeled benzene; static system, declining exposure, 48 h; 25 females only; linear decrease in benzene concentration to approximately 10% of initial concentration remaining at end of 48 h.

All benzene exposures were terminated and open flow reestablished in the 100 ppb static exposure tank at the end of 48 h. The static exposure of ^{14}C-labeled benzene was to determine the uptake, accumulation, and depuration of benzene in the gonads of females. The open flow constant exposure and control were primarily to establish morphological and mortality effects on the ovarian eggs and delayed effects on subsequent larval development and mortality.

The behavior of fish was observed before sampling. Subsamples of females were taken daily for 6 days—2 days during exposure and 4 days after. Fish were removed randomly until 10 females were obtained from the control and 800 ppb exposure conditions. Five females were removed daily from the static 100 ppb exposure. Concentrations of benzene in the water of all tanks were also measured daily.

Each female sampled was measured (standard length), weighed (wet weight), and the ovaries dissected out. The ovaries were also measured (total length) and weighed (wet weight); the left ovaries were examined microscopically, the right

[3]Eldridge, M. B., T. Echeverria, and J. W. Struhsaker. Manuscr. in prep. The effect of benzene on the energetics of Pacific herring (*Clupea harengus pallasi*) embryos and larvae.

[4]Benville, P., Jr., and S. Korn. Manuscr. in prep. The acute toxicity of six mono-cyclic aromatics to striped bass (*Morone saxatilis*) and bay shrimp (*Crago* sp.).

ovaries prepared for radiometric or gas chromatograph analyses. Methods of preparation for radiometric and chromatograph measurements are described elsewhere (Benville and Korn 1974; Korn, Hirsch, and Struhsaker 1976, see footnote 2). It should be emphasized that the radiometric technique measures total radioactivity and concentrations calculated may include metabolites of benzene as well as benzene itself.

Ovaries were examined under a dissecting microscope for developmental stage [Hjort's stage (Bowers and Holliday 1961)] and the presence of opaque dead or dying eggs, and the gross appearance (color and degree of deliquescence) was ranked. The maximum diameters of 10 eggs from the ovary of each female were measured and the eggs examined for abnormal development.

On day 3, after cessation of exposure, pieces of clean plastic screening were placed around the standpipe in the center of the 800 ppb and 100 ppb exposure and control tanks to provide substrate for spawned eggs. Males were placed with females in the 100 ppb tank. After spawning occurred, the screens were removed and eggs examined for developmental stage and mortality. Pieces of screen with 75 eggs on each (most in 4-cell stage) were cut apart. Pieces of screen were selected with a single layer of relatively separated eggs because previous experience showed reduced survival in dense egg clusters. Two pieces of screen with 75 eggs each were placed in each 8-liter rearing container (total of 150 eggs). There were five replicate containers for each treatment and control (total of 15 containers). Temperature during development was 11.0°-12.0°C, and salinity, 22.0‰. Other rearing conditions were as previously described (Struhsaker et al. 1974). Hatching occurred 10 days after fertilization, and percent survival at hatching was determined from three replicate counts of swimming larvae in each container and by counting the number of dead and abnormal embryos left on the screen. The screens were removed and surviving larvae fed the rotifer, *Brachionus plicatilis,* through the remainder of the experiment (past yolk absorption to larval day 7). Surviving larvae were counted and the percent survival through yolk absorption determined from the original egg number.

Data were analyzed, depending upon variables, with the methods of analysis of variance and covariance using University of California Biomedical programs, BMD 01V, 02V, and 03V (Dixon 1970).

RESULTS

No adult mortalities occurred during the 6 days of the experiment. Stress behavior was noted in exposed fish, particularly at the constant 800 ppb exposure. Definite distress was observed by the end of the first day, although oxygen levels were above saturation. Milling was disrupted, fish were gaping at the surface, and many exhibited disequilibrium. Even after cessation of exposure, stress behavior continued for the duration of the experiment. Control fish may also have been stressed by the capture conditions and the short acclimation period, but they exhibited none of the stress symptoms of exposed fish and milled normally.

Although behavior was abnormal in exposed fish, spawning occurred in the tanks. In fact, the stress from benzene exposure appeared to prematurely induce spawning. This is illustrated in Table 1 by the percentage of exposed fish which were spent (Stage VII) compared with control fish. At the end of the 6-day experimental period, 73% (100 ppb) and 70% (800 ppb) of the exposed fish were spent, compared with only 25% of the controls. The higher percentage of spent females in the 100 ppb static treatment than in the 800 ppb open flow treatment during the first 4 days may be a result of additional stress imposed by static conditions. At all treatments, most unspent ovaries were ripe (Stage VI); only 7-10% were immature (Stages III-V) (Table 1).

No changes in growth (as indicated by wet weight and length) were expected in females over the short experimental period. However, these measurements were taken to determine the similarity of fish between the treatments and to adjust effect of size on the differences in weights of ovaries between the treatments. Ovary length and weight and egg diameters were measured to determine if benzene uptake affected the growth or resorption of ovaries or eggs and to determine the ripeness or proximity to spawning. Data are summarized in Table 2. Egg diameter did not correlate with any other measurement variable. Analysis of variance revealed no significant difference ($P>0.25$) in egg diameter between 0 and 800 ppb benzene treatments. Since the size range of females varied somewhat between the two treatments (Table 2), analysis of covariance was used to compare the weights of females and ovaries between concentrations and days after adjustment for the effect of lengths (Table 3). No

TABLE 1.—Effects of benzene exposure on ovaries and eggs of Pacific herring.

Hours (Days)	Benzene concentration (nl/l; ppb)	No. of ovaries examined	Percent of eggs in stage[1] III-V Immature	VI Ripe	VII Spent	No. of ripe ovaries examined	Stages III-VI dead eggs No.	%
24	0	10	10	80	10	9	0	0
(1)	100	5	0	40	60	2	0	0
	800	9	40	49	11	8	0	0
48	0	10	0	90	10	9	0	0
(2)	100	5	0	20	80	1	1	100
	800	10	10	60	30	7	1	14
72	0	10	20	70	10	9	0	0
(3)	100	5	20	40	40	2	2	100
	800	9	0	56	44	6	6	100
96	0	10	0	70	30	7	1	14
(4)	100	5	20	20	60	1	1	100
	800	10	10	57	33	6	6	100
120	0	10	10	40	50	5	0	0
(5)	100	5	0	0	100	0-All spent	—	—
	800	9	0	0	100	0-All spent	—	—
148	0	10	0	60	40	6	0	0
(6)	100	5	0	0	100	0-All spent	—	—
	800	10	0	0	100	0-All spent	—	—
Totals	0	60	7	68	25	36	1	3
(6 days)	100	30	7	20	73	6	4	67
	800	57	10	20	70	24	13	54

[1]Hjort's stage; Bowers and Holliday (1961).

TABLE 2.—Mean and range of female standard length, wet weight; ovary length and wet weight; and maximum egg diameter for Pacific herring. Linear equation describes the regression of wet weights on lengths for both whole female fish and left ovaries. Sample size = 59 females; 59 ovaries (spent females excluded).

Benzene concentration (ppb)	Female: Standard length (*X*) Range (cm)	Mean (cm)	Female: Wet weight (*Y*) Range (g)	Mean (g)	Ovary (Stages III-VI): Total length (*X*) Range (cm)	Mean (cm)	Wet weight (*Y*) Range (g)	Mean (g)	Max egg diameter Range (mm)	Mean (mm)
0	16.8-22.4	19.3	76.8-239.6	136.8	7.7-11.5	10.4	6.7-30.8	18.2	1.20-1.50	1.30
800	16.4-21.5	18.7	75.3-189.6	120.3	7.5-14.3	9.3	6.3-26.5	13.6	1.20-1.56	1.30
Total	16.4-22.4	19.0	75.3-239.6	126.2	7.5-14.3	9.9	6.3-30.8	15.9	1.20-1.56	1.30
	Regressions[1]									
0	$\hat{Y} = -339.96 + 24.98X$				$\hat{Y} = -19.26 + 3.56X$					
800	$\hat{Y} = -267.50 + 20.89X$				$\hat{Y} = -12.84 + 2.90X$					

[1]Tests of significance between slopes (*b*) and elevations (*a*) of regressions showed no significant difference ($0.100 < P < 0.250$) between concentrations (Snedecor and Cochran 1967:432-436).

TABLE 3.—Analysis of covariance of wet weight on standard length of female, wet weight of ovary on wet weight of female, and wet weight on total length of ovary for Pacific herring. Analysis of ripe ovaries (Stage VI) only. Treatments: Concentrations (0 vs. 800 ppb); Days (1 to 4); 2×4=8 treatment combinations × 5 observations per treatment combination = 40.

Analysis of dependent variable (wet wt female) after adjustment for covariate (standard length female)						
Source of variation	df	SS	MS	*F* ratio[1]	Probability	
Between concentrations (C) (0 vs. 800 ppb)	1	5.2508	5.2508	0.24	$P > 0.250$	NS[2]
Between days (D)	3	675.2348	225.0783	1.04	$P > 0.250$	NS
Interaction (CD)	3	485.9035	161.9678	0.75	$P > 0.250$	NS
Within cells	31	6,721.2742	216.8153			
Analysis of dependent variable (wet wt ovary) after adjustment for covariate (wet wt female)						
Source of variation	df	SS	MS	*F* ratio	Probability	
Between concentrations (C) (0 vs. 800 ppb)	1	0.6940	0.6940	0.13	$P > 0.250$	NS
Between days (D)	3	2.5351	0.8450	0.16	$P > 0.250$	NS
Interaction (CD)	3	19.4057	6.4686	1.21	$P > 0.250$	NS
Within cells	31	165.5181	5.3393			
Analysis of dependent variable (wet wt ovary) after adjustment for covariate (total length ovary)						
Source of variation	df	SS	MS	*F* ratio	Probability	
Between concentrations (C) (0 vs. 800 ppb)	1	0.4585	0.4585	0.04	$P > 0.250$	NS
Between days (D)	3	27.2532	9.0844	0.71	$P > 0.250$	NS
Interaction (CD)	3	8.0860	2.6953	0.21	$P > 0.250$	NS
Within cells	31	398.2616	12.8471			

[1]$F\ 0.05 = 4.16$, df = 1,31; $F\ 0.05 = 2.91$, df = 3,31.
[2]NS = not significant.

significant difference ($P>0.25$) between concentrations or days or interaction was found. Tests between slopes (b) and elevations (a) of the regression lines of weights on lengths of females and weights on lengths of ovaries (Snedecor and Cochran 1967:432-436) showed no significant differences ($P>0.10$) between 0 and 800 ppb concentrations (Table 2).

Microscopic examination of the ovaries, however, revealed the presence of dead eggs in ovaries of exposed fish by the second day of exposure (Table 1). No dead eggs were found in control fish until day 4, and then only a few (15-20 eggs) in one female, the rest of the ovary appearing normal. Ovaries of exposed fish contained significantly larger numbers of opaque dead eggs (more than 10%) and were generally paler yellow and deliquescent. By the end of 6 days, 67% (100 ppb) and 54% (800 ppb) of exposed females were found with ovaries containing dead or dying eggs.

The uptake and depuration of benzene in ovaries of females exposed to a static initial concentration of 100 nl/liter (ppb) ^{14}C-labeled benzene is shown in Figure 1, together with data determined from other larval studies for later stages (Eldridge, Struhsaker, and Echeverria[5]). Uptake was rapid, so that a maximum accumulation (1.4 μl/g; ppm) was reached in 24 h. This level was maintained through the 48-h exposure period. After open flow was reestablished and exposure ended, benzene and/or metabolites were depurated until they reached an undetectable level in 96 h. The figure shows that levels accumulated in ovarian eggs were higher and sustained longer than in later egg and larval stages from other experiments with comparable exposure conditions.

Results of rearing experiments with eggs from females exposed to 0 and 800 ppb unlabeled benzene are summarized in Tables 4 and 5. Survival was also reduced in eggs and larvae from females exposed to an initial concentration of 100 ppb labeled benzene. However, results were obscured by an additional variable. Eggs taken from the static exposure tank were covered by filamentous bacterial growth early in development and many eggs died as a result. In the other treatment with open flow and in controls, eggs did not undergo this mortality due to epifloral growth.

[5]Eldridge, M. B., J. W. Struhsaker, and T. Echeverria. Manuscr. in prep. The uptake, accumulation and depuration of ^{14}C-labeled benzene in embryos and larvae of Pacific herring (*Clupea harengus pallasi*).

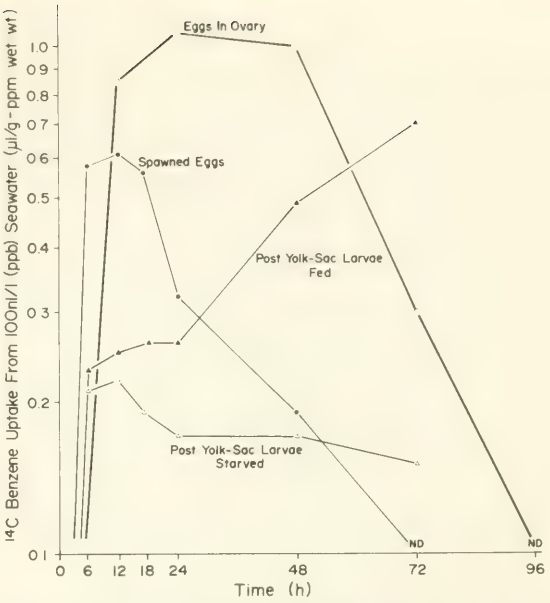

FIGURE 1.—Accumulation of ^{14}C-labeled benzene in different early Pacific herring developmental stages exposed to an initial concentration of 100 nl/liter (ppb) in a static system. Concentrations shown on y-axis were calculated from total radioactivity and may include metabolites derived from benzene as well as benzene. Spawned eggs were in a stage just prior to blastopore closure; post yolk-sac larvae were fed the rotifer, *Brachionus plicatilis*, containing high accumulated levels of labeled benzene. ND = not detectable.

The 100 ppb treatment, therefore, was not included in the analysis. Analysis of variance showed survival at hatching and survival of larvae through yolk absorption were significantly less in exposed eggs (800 ppb) than in control eggs ($P<0.1$; Table 5). Exposure to ppb benzene levels for only 48 h reduced survival by about 43% through yolk absorption to larval day 7 (Table 4).

DISCUSSION

When female herring were briefly exposed to low levels of benzene for 48 h just prior to spawning, a significant reduction occurred in survival of eggs and resultant larvae from the ovary through yolk absorption. It is probable that further mortality would have occurred in later larval stages if the experiments were continued. When this result is compared with that from exposing other life history stages after spawning (Struhsaker et al. 1974; Eldridge et al. see footnote 5) where survival is not affected except at ppm levels, it appears that the spawning female and ovarian eggs are the most sensitive stages.

TABLE 4.—Mean percent survival through hatching and yolk absorption of Pacific herring larvae from eggs of benzene-exposed and control females.

Stage	Benzene concentration (nl/l; ppb)	Total no. of eggs	Mean survival (%)	95% confidence interval (%)	Mean reduction survival[1] (%)
Embryos to hatching	0	750	92.9	91.5-94.3	
	800	750	66.6	64.1-69.1	−26.3
Hatched larvae through yolk absorption	0	750	76.7	74.5-78.9	
	800	750	34.4	32.0-36.8	−43.3

[1]See Table 5 for test of significance.

TABLE 5.—One-way analysis of variance in survival of Pacific herring embryos to hatching and larvae through yolk absorption (larval day 7). Ripe females exposed prior to spawning. Five replicate containers per treatment; 150 eggs/container. (Arcsin transformation applied to percent survival data.)

Percent survival to hatching					
Source of variation	df	SS	MS	*F* ratio	Probability
Between concentrations 0 vs. 800 ppb	2	1.3442	0.6721	95.6098**	$P<0.01$
Within groups	12	0.0843	0.0070		
Total	14	1.4285			
Percent survival through yolk absorption					
Source of variation	df	SS	MS	*F* ratio	Probability
Between concentrations 0 vs. 800 ppb	2	0.8053	0.4026	30.2147*	$P<0.05$
Within groups	12	0.1599	0.0133		
Total	14	0.9652			

Although male herring were not studied in detail here, their behavior was severely disrupted, as in the females. Testes of mature, spawning herring have been found to contain higher levels of cholesterol (a lipid) during spawning than at other times in their adult life (Blaxter and Holliday 1963), and it is possible the lipid-soluble benzene may accumulate to high levels in testes of ripe males. Effects on males and their spermatozoa, as well as effects on females, may have contributed to reduction in survival of fertilized eggs through yolk absorption in these experiments.

Reference to Figure 1 shows that the maximum accumulation of labeled benzene in ovarian eggs was greater than in later egg and larval stages as measured in other experiments. Accumulation in ovarian eggs of exposed females was approximately twice that in eggs exposed just after spawning and prior to blastopore closure and about six times that in embryos exposed just after yolk-sac absorption. Accumulation for the first 48 h of water column exposure in these stages appears to correlate with the yolk volume of the eggs and larvae, decreasing as yolk is utilized, as would be expected with lipid-soluble benzene. However, the decreased accumulation may also relate to the development of enzymes enabling later stages to metabolize benzene and subsequently depurate more rapidly. After being fed *Brachionus plicatilis,* which accumulate high levels of benzene (Echeverria[6]), the fish larvae rapidly accumulated benzene from their food (Figure 1). Other studies of accumulation in tissues of adult herring (Korn et al. see footnote 2) show that only one site, the gall bladder with bile, accumulates higher concentrations than ovarian eggs (30 times and 14 times initial concentration, respectively).

I have noted previously (Struhsaker et al. 1974) that the percentage survival of eggs through hatching is significantly less (approximately 25% less; $P<0.01$) in Pacific herring eggs collected from San Francisco Bay than in those from Tomales Bay. Although other environmental differences may be involved, this reduction in hatching success may well relate to the effects of accumulated pollutants in the gonads of spawning fish in the relatively more polluted San Francisco Bay waters and warrants further study.

Estimating that the reduction in survival of eggs through yolk absorption of spawning exposed females is at least 43%, the effect on Pacific herring populations exposed to only one toxic component of petroleum could be significant. Considering that the total water-soluble fraction contains many other toxic aromatics, it is possible

[6]Echeverria, T. Manuscr. in prep. Uptake and depuration of ^{14}C benzene in the rotifer, *Brachionus plicatilus.*

that long-term chronic exposures to low levels may be decreasing population survival in polluted areas. In addition, chlorinated hydrocarbons in pesticides may also be accumulating in the gonadal lipids and interacting with petroleum hydrocarbons producing even more deleterious effects. More studies of the effects of these components on spawning fish are clearly needed. If fishes prove generally to be the most sensitive to accumulated oil components during their spawning season, fisheries management decisions should take into consideration their protection from damaging levels, particularly at spawning time.

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BIOLOGY OF THE REX SOLE, *GLYPTOCEPHALUS ZACHIRUS*, IN WATERS OFF OREGON

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ABSTRACT

Data are presented on the life history and population dynamics of rex sole, *Glyptocephalus zachirus* Lockington, collected from Oregon waters between September 1969 and October 1973. Length-weight relationships vary little between sexes or with time of year. Otolith annuli form primarily from January through May and were used for age determination. Age and length are highly correlated (r = 0.9945 for males and 0.9864 for females), with females growing faster and living longer than males. Estimates of total instantaneous mortality rate (Z) appear less variable when calculated by the catch-curve method (mean Z of 0.64 for males and 0.51 for females), than by the Jackson method. Age at 50% maturity occurs at 16 cm (about 3 yr) for males and at 24 cm (about 5 yr) for females. Spawning off northern Oregon occurs from January through June, with a peak in March-April. Fecundity is correlated (r = 0.9620) with length of fish. There were 15 recaptures (0.59%) from 2,537 fish tagged off northern Oregon during March and June 1970. Maximum movement of recaptured fish was only 53.9 km, but the low recovery precludes definite conclusions. Twenty loci were detected by starch-gel electrophoretic analysis using rex sole muscle tissue. Of these, three loci were polymorphic, but showed no discernible variation between collections from northern, central, and southern Oregon in April 1973.

Investigation into the life history of rex sole, *Glyptocephalus zachirus* Lockington, by the Oregon Department of Fish and Wildlife provided new information on this species. The broad objective was to develop knowledge of the biology and population dynamics of rex sole found off the Oregon coast which would enhance management of this species.

Specific objectives were to: 1) determine the length-weight and age-length relationships; 2) estimate the total instantaneous mortality rate by two independent methods; 3) determine relationships of maturity and fecundity with length and age, and with the spawning season; and 4) determine if rex sole off Oregon are composed of separate stocks[3] which undergo predictable movements.

The rex sole is a slender, thin flatfish belonging to the family Pleuronectidae (Starks 1918; Norman 1934), the right-eyed flounders. Of the three species of *Glyptocephalus*, rex sole is the only one reported in the eastern Pacific Ocean (Pertseva-Ostroumova 1961). Geographically distributed from southern California to the Bering Sea (Miller and Lea 1972), it is found bathymetrically to 730 m (Alverson et al. 1964). Rex sole is important in the commercial trawl fishery from California northward through British Columbia. In 1972, rex sole was the fifth most important flatfish in weight (1.54 million kg [3.4 million pounds]) in the domestic northeastern Pacific trawl food fishery. *Glyptocephalus zachirus* is also important in the domestic trawl fishery for animal food (Best 1961; Niska 1969), although this fishery has declined in recent years. On the continental shelf off the northern three-fourths of the Oregon coast, rex sole was third in biomass[4] and first in numbers of all flatfish caught with an 89-mm (3.5-inch) mesh trawl.

There is little published information on the biology of rex sole. Villadolid (1927) and Frey (1971) reported briefly on the time of spawning, size and age at maturity, and food habits for specimens captured off California. Hart (1973) summarized the life history of rex sole off Canada and suggested that the lack of information resulted in doubtful deductions. An aging study was conducted on rex sole by Villadolid (1927) who used scales. Domenowske (1966) used otoliths,

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[3]The rex sole spawning in a particular marine location (or portion of it) at a particular season, and which do not interbreed to a substantial degree with any group spawning in a different place, or in the same place at a different season (modified from Ricker 1972).

[4]Demory, R. L., and J. G. Robinson. 1973. Resource surveys on the continental shelf of Oregon. Fish Comm. Oreg., Commer. Fish. Res. Dev. Act Prog. Rep., July 1, 1972 to June 30, 1973, 19 p. (Unpubl. manuscr.).

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scales, and interopercles for aging rex sole; by comparing the age-length relationships, he concluded otoliths were the most readable structure. Vanderploeg (1973) conducted food habit studies on rex sole collected off Oregon. Porter (1964) described the larvae of rex sole, and Waldron (1972) and Richardson (1973) reported on distribution and abundance of rex sole larvae. Tsuyuki et al. (1965) conducted a general starch-gel electrophoresis study on the muscle proteins and hemoglobin of 50 species of North Pacific fish and found that rex sole differed from 10 other pleuronectids tested. Benthic distribution of rex sole was investigated by numerous workers[4] (Alverson et al. 1964; Day and Pearcy 1968; Demory 1971; Alton 1972). Limited tagging studies (Manzer 1952; Harry 1956) were conducted to determine movements of rex sole, but no tagged fish were recaptured.

METHODS

Rex sole were collected by otter trawl off Oregon from the Columbia River south to Cape Blanco at depths of 18-200 m during September 1969-73. Most data were obtained from rex sole captured incidentally to a study of pink shrimp, *Pandalus jordani*, distribution during 1969-70.[5] Rex sole were also obtained from commercial trawl landings at Astoria, Oreg., in 1970 and 1973; at Charleston and Brookings, Oreg., in 1973; and from research vessel catches during the 1971-73 Fish Commission of Oregon (FCO) groundfish surveys.[4,6] All specimens were frozen until time of examination.

Rex sole were sexed by examination of gonads, measured for total length (TL) to the nearest centimeter, and weighed to the nearest gram. The left otolith was removed for aging studies, stored in a 50:50 solution of glycerin and water, and read using reflected light on a dark background (Powles and Kennedy 1967).

The length-weight relationship, by calendar quarters, of rex sole collected off central and northern Oregon in 1969-72 was determined by the least squares method using the logarithmic form of the equation $W = aL^b$, where W is weight in grams, L is length in centimeters, and a and b are constants.

Estimates of the lineal growth of rex sole were obtained from the age-length relationship of fish collected off northern Oregon in September-October 1969 and September 1971. A mean total length (TL) at each age was determined from these data and expressed mathematically in terms of the von Bertalanffy growth equation (Ricker 1958; Ketchen and Forrester 1966).

To obtain the calculated growth parameters, we used ages 1.5-10.5 yr for males and 1.5-12.5 yr for females.

Estimates of the instantaneous total mortality rate (Z) were made using age group data obtained from FCO groundfish cruises off northern Oregon in 1971 and 1973 and off central Oregon in 1972. Two methods, a catch curve (Ricker 1958) and the Jackson technique (Jackson 1939), were used for the analyses.

To determine maturity stages, gonads were examined according to the procedures described by Hagerman (1952), Scott (1954), and Powles (1965). Definitions used for maturity stages are listed in Table 1.

Fecundity was determined from 13 fish collected in February 1970 and measured to the nearest millimeter (TL). Both ovaries were removed from

TABLE 1.—Description of reproductive phases of rex sole gonads used in this study.

Sex	Maturity stage	Description
Females	Immature	(A): Ovaries very small (<40 mm TL), whitish in color, semitransparent, and gelatinous. No eggs discernible to the naked eye.
	Mature	(B): Ripening. Ovaries enlarging, becoming reddish-orange colored and granular in consistency, full of developing eggs that can be recognized by direct observation.
		(C): Ripe. Ovaries full of mostly reddish-orange colored granular eggs, although a few transparent ova are present. Ova can be extruded from the fish by using considerable pressure.
		(D): Spawning. Ovaries full of entirely translucent eggs which will run with slight pressure.
		(E): Spent. Ovaries flaccid, usually empty although occasionally a few eggs will remain. Ovarian membrane very transparent and saclike.
		(F): Recovering. Ovaries filling with fluid, and reddish-orange in color. No ova detectable to the naked eye.
Males	Immature	(A): Testes very small (<3 mm TL), translucent in color and not extending into the abdominal cavity.
	Mature	(B): Ripening. Testes enlarged, extending posteriorly into abdominal cavity, light brown to cream colored, but retain sperm under pressure.
		(C): Ripe and/or spawning. Testes full and cream colored. Sperm will run under no or only slight pressure.
		(D): Spent-recovering. Testes shrunken and transparent or dark brown in color.

[5]Lukas, G., and M. J. Hosie. 1973. Investigation of the abundance and benthic distribution of pink shrimp, *Pandalus jordani*, off the northern Oregon coast. Fish Comm. Oreg., Commer. Fish. Res. Dev. Act, Final Rep., July 1, 1969 to June 30, 1970, 45 p. (Unpubl. manuscr.).

[6]Demory, R.L. 1974. Resource surveys on the continental shelf of Oregon. Fish Comm. Oreg., Commer. Fish. Res. Dev. Act Prog. Rep., July 1, 1973 to June 30, 1974, 6 p. (Unpubl. manuscr.).

each fish and stored in 10% Formalin.[7] Estimates of fecundity were obtained gravimetrically, following the method described by Harry (1959).

To obtain fish for tagging, short tows of about 15 min were made in March and June 1970 off northern Oregon near the mouth of the Columbia River. Any rex sole caught were held for 15-60 min in a tank containing running seawater. Fish in good condition were tagged and released. Petersen disc (vinyl) tags, 16 mm in diameter, were attached by a stainless steel pin inserted through the musculature about ½ inch below the midbase of the dorsal fin. Fishermen were advised of the tagging program, and a $0.75 reward was offered by the FCO for each tagged rex sole returned.

Electrophoresis was used to investigate stock identification of rex sole. A preliminary electrophoretic examination was conducted using muscle tissue of 145 rex sole collected in April 1973 in three nearly equal samples taken off northern, central, and southern Oregon. Tissue extraction and starch gel electrophoresis procedures followed the methods of Johnson et al. (1972). Tests were conducted for polymorphisms in muscle protein and the five enzyme systems: aspartate aminotransferase (AAT) A-I and A-II; lactic dehydrogenase (LDH); peptidase A-I and A-II; phosphoglucomutase (PGM); and tetrazolium oxidase (TO).

RESULTS AND DISCUSSION

Length-Weight Relationships

Length and weight were closely correlated, with the derived coefficient of determination (r^2) varying from 0.9902 to 0.9988 for males and from 0.9872 to 0.9966 for females (Table 2). These coefficients of determination varied little by season, possibly because of the extended spawning period (Villadolid 1927) in the first half of the year. Based on data in Table 2, we calculated mean weights by season at representative lengths. For both sexes weight increase was greatest in the third quarter, average in the second quarter, and slowest in the first and fourth quarters (Table 3). Among mature fish, about 30 cm TL and larger, females generally were slightly heavier than males of the same length (Figure 1). A total of 950 males and 1,121 females were included in the length-weight data analyzed.

Age and Growth

Validity of the Aging Technique

Opaque or hyaline zones occur on the margin of rex sole otoliths. These zones mark the respective periods of rapid or slow growth. Examination of 265 otoliths from rex sole <27 cm TL collected off northern Oregon from September 1969 through July 1970 revealed that hyaline edges were first observed in September (Figure 2). No hyaline edges were present the previous June or July. In the fall the percentage of otoliths with a hyaline zone on their edge began to increase. By January the majority of otoliths had a hyaline zone on their edge. The percentage rapidly increased and peaked in March when 92.3% had hyaline zone margins. Conversely, opaque zones on edges were at their lowest in March, gradually increasing until June or July when all otoliths had opaque edges.

[7]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Length-weight relationship ($\log_{10} W = \log_{10} a + b \log L$) by quarterly period for male and female rex sole collected off central and northern Oregon, 1969-72.[1]

Period and sex	Number of fish	Constant log a	Constant b	Standard deviation	Correlation coefficient	Coefficient of determination
January-March:						
Male	119	−3.1447	3.5551	0.1437	0.9972	0.9944
Female	68	−3.0978	3.5095	0.1587	0.9936	0.9872
Both	187	−3.1248	3.5258	0.1539	0.9932	0.9864
April-June:						
Male	386	−2.8398	3.3557	0.1501	0.9994	0.9988
Female	356	−2.9398	3.4345	0.1488	0.9980	0.9960
Both	742	−2.8903	3.3914	0.1567	0.9984	0.9968
July-September:						
Male	350	−3.0884	3.5598	0.1461	0.9982	0.9964
Female	621	−2.9886	3.5112	0.1661	0.9983	0.9966
Both	971	−3.0631	3.5553	0.1788	0.9988	0.9976
October-December:						
Male	95	−2.9823	3.4423	0.1269	0.9951	0.9902
Female	76	−2.9795	3.4423	0.1599	0.9972	0.9944
Both	171	−2.9500	3.4252	0.1562	0.9973	0.9946

[1]Regression analysis conducted on 11- to 36-cm males and 11- to 51-cm females.

TABLE 3.—Computed mean weight per quarter at selected lengths of male and female rex sole, using regression formulas from Table 2.

Sex	Total length (cm)	Computed mean weight (g) per quarter[1] I	II	III	IV
Male	15	11	13	13	12
	25	67	71	77	68
	35	221	220	256	215
Female	15	11	13	14	12
	25	64	73	83	68
	35	210	231	271	231
	45	506	547	655	514

[1]I = Jan.-Mar.; II = Apr.-June; III = July-Sept.; IV = Oct.-Dec.

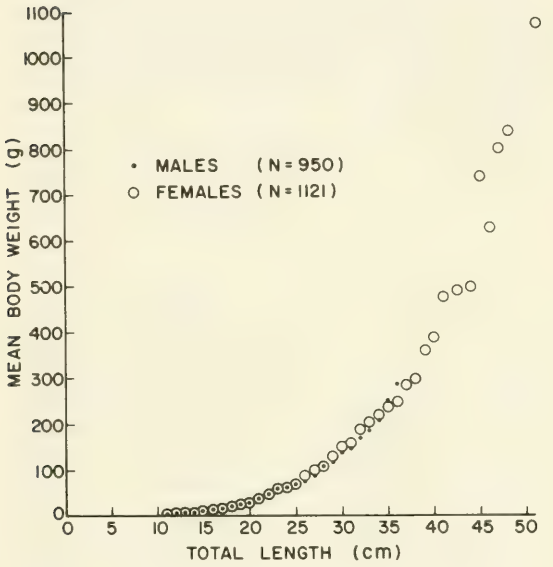

FIGURE 1.—Length-weight relationship for male and female rex sole collected off central and northern Oregon, 1969-72. Body weights obtained from an average of quarterly mean values.

From these observations, we concluded that the hyaline margin is deposited on otoliths during each winter and spring for all sizes of rex sole. Thus, these hyaline zones are interpreted as annuli with a year's growth occurring between successive hyaline margins. These results are similar to those of Villadolid (1927) who found northern California rex sole formed a scale annulus in March through May.

Age-Length Relationship

After 3.5 yr of age, females were consistently longer than males at a given age. Females also attained an older age and longer length. Statistics for both males and females followed the von Bertalanffy growth curve, as a good fit was obtained for most age groups (Figure 3, Table 4).

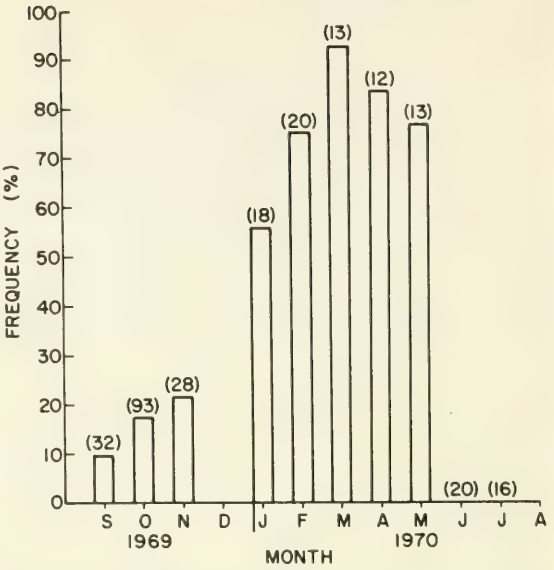

FIGURE 2.—Percent frequency of hyaline edges found on otoliths of 265 rex sole (<27 cm TL) collected off northern Oregon, September 1969-July 1970. Numbers in parentheses represent sample size.

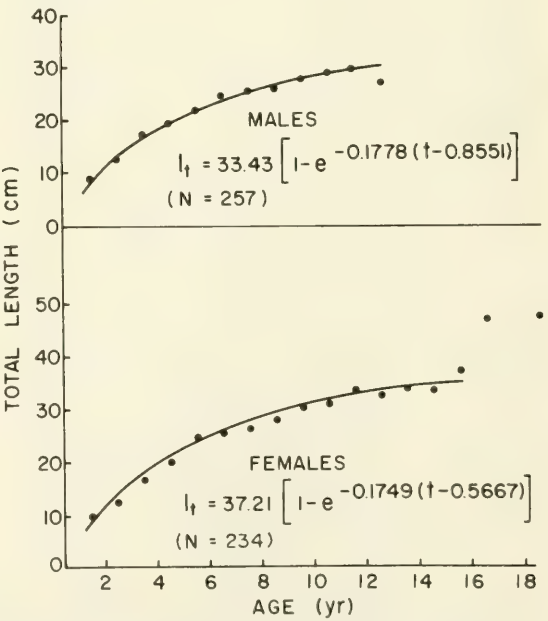

FIGURE 3.—Age-length relationship for male and female rex sole collected off northern Oregon, September-October 1969 and September 1971.

The calculated length at infinity (L_∞) of 33.43 cm for males was close to the computed mean value of 29.33 cm (Table 4). For females the L_∞ of

TABLE 4.—Computed mean length at age and mean length at age estimated by von Bertalanffy growth equation for 45 unsexed, 189 male, and 212 female rex sole collected off northern Oregon in September-October 1969 and September 1971.

Age[1] (yr)	Male No.	Male Computed mean length (cm)	Male Estimated mean length[2] (cm)	Female No.	Female Computed mean length (cm)	Female Estimated mean length[2] (cm)
1.5	[3]45	9.20	9.44	[3]45	9.20	8.91
2.5	13	12.61	13.36	7	12.71	13.44
3.5	36	17.00	16.65	33	16.64	17.25
4.5	29	19.52	19.39	11	20.45	20.45
5.5	15	21.66	21.69	19	24.95	23.14
6.5	17	24.55	23.62	14	25.64	25.39
7.5	23	25.39	25.22	9	26.33	27.29
8.5	23	25.82	26.57	17	28.05	28.88
9.5	16	27.37	27.69	24	30.37	30.21
10.5	10	28.90	28.63	28	31.03	31.34
11.5	6	29.33	29.42	20	33.35	32.28
12.5	1	27.00	30.07	14	32.45	33.07
13.5				4	33.75	33.73
14.5				2	33.50	34.29
15.5				6	37.00	34.76
16.5				1	47.00	
17.5				0	0.00	
18.5				3	47.30	

[1]These fall-caught fish were assumed to be about one-half way through the growing season, based upon otolith readings.

[2]Von Bertalanffy growth equations were based on 1- to 10-yr-old males (L_∞ = 33.43 cm, K = 0.1778, t_0 = −0.8551 yr), and 1- to 12-yr-old females (L_∞ = 37.21 cm, K = 0.1747, t_0 = −0.5667 yr).

[3]Sexes were not separated for age 1 fish (45 specimens).

37.21 cm fit observed data through age 15.5, but was far below the maximum computed mean TL of 47.30 cm. The apparent discrepancy does not invalidate the data because Knight (1968) noted that L_∞ is not the maximum obtainable length, but rather a mathematical tool needed in computations for the von Bertalanffy growth equation. This is exemplified by our collection of a 23-yr-old (±1 yr), 59-cm female rex sole off northern Oregon in February 1970, which we consider as about the maximum length and age of rex sole. Hart (1973) reported a 24-yr-old rex sole was collected off British Columbia, but no length was given.

Mortality Rate

Estimates of the total instantaneous mortality rate (Z) derived from data in Table 5 and using the catch curve method varied from 0.53 to 0.70 for males and from 0.44 to 0.55 for females (Table 6). In this analysis the natural logarithm of the numbers of males and females caught at each age was plotted against the respective age class (Figures 4, 5). The total mortality rate was the best fitted slope on the right side of the catch curve, determined by linear regression using ages ranging maximally from 6 to 16 yr (Table 5).

Estimates of Z using the Jackson method ranged from 0.43 to 0.61 for males and from 0.20 to 0.52 for females (Table 6). In this method annual survival rate (S) is:

TABLE 5.—Numbers of rex sole per age group caught during groundfish surveys off northern Oregon in 1971 and 1973 and central Oregon in 1972.

Age (yr)	Number males 1971	1972	1973	Number females 1971	1972	1973
2	7	14	11	0	19	26
3	50	68	75	59	70	116
4	67	142	45	102	124	56
5	270	290	337	353	207	514
6	244	663	387	329	732	613
7	375	278	881	418	501	1,217
8	380	412	432	400	560	570
9	215	274	382	366	465	596
10	320	45	106	582	108	201
11	67	123	42	138	283	94
12	76	24	72	247	32	219
13	5	14	11	69	57	30
14	10	2	0	50	10	26
15	5	7	0	20	10	0
16	2	2	0	7	3	9
18				9	3	0
21						4
Total	2,093	2,358	2,781	3,149	3,184	4,291

TABLE 6.—Estimates of the total instantaneous mortality rate (Z) of rex sole collected off northern Oregon in September 1971 and 1973 and off central Oregon in September 1972.

Year and sex	Age of maximum numbers	Ages utilized	Catch curve estimates of Z	Jackson method estimates of Z
1971:				
Male	8	8-16	0.70	0.43
Female	10	7-16	0.44	0.20
1972:				
Male	6	6-13	0.53	0.44
Female	6	6-16	0.55	0.31
1973:				
Male	7	7-13	0.68	0.61
Female	7	7-14	0.54	0.52
Mean:[1]				
Male			0.64	0.49
Female			0.51	0.34

[1]Based on simple average of Z's for the 3 yr.

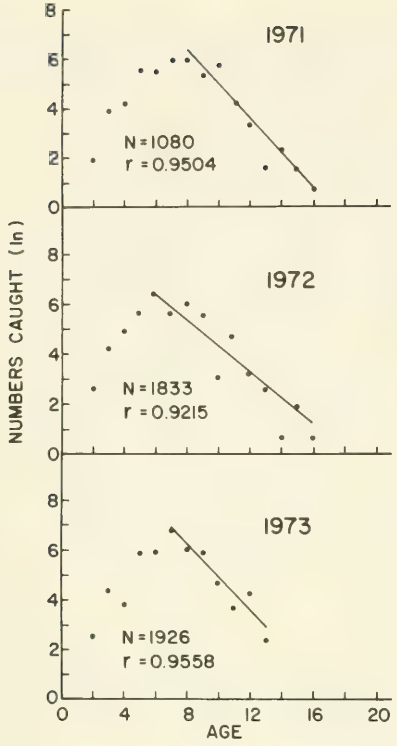

FIGURE 4.—Catch curves of male rex sole collected off Oregon in September 1971, 1972, and 1973.

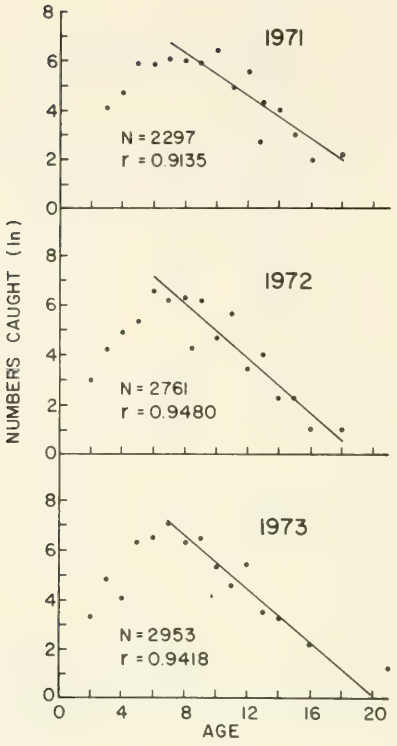

FIGURE 5.—Catch curves of female rex sole collected off Oregon in September 1971, 1972, and 1973.

$$S = \frac{N_7 + N_8 + \ldots + N_r}{N_6 + N_7 + \ldots + N_{r-1}}$$

where N is the number of fish of age group r caught. Annual mortality rate is $1 - S$ and the corresponding instantaneous rate of total mortality is obtained from the expression $S = e^{-z}$, where e and Z are derived from Ricker (1958).

The catch curve method probably gives more reliable estimates of Z than those obtained using the Jackson method. In the Jackson method the larger samples of younger fish strongly affect the estimates, with the older age groups weighted less. Thus, the Jackson method substantially underestimates the mean Z for the entire right limb of the catch curve.

Reproduction

Size at Maturity

Some males were mature at 13 cm while no females reached maturity until 19 cm (Figure 6).

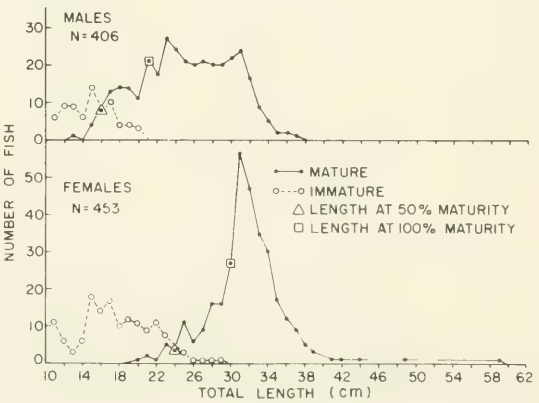

FIGURE 6.—Size composition of immature and mature rex sole, by sex, collected off northern Oregon, September 1969-July 1970.

About 50% of the males were mature at 16 cm, and all were mature at 21 cm. For females, 50% were mature at 24 cm and 100% were mature at 30 cm. Lengths at 50% and 100% maturity correspond to

about ages 3 and 5 for males and 5 and 9 for females (Table 4).

The only maturity data on rex sole available from other areas is that of Villadolid (1927). He found that both males and females off San Francisco, Calif., were fully mature at age 4, which corresponded to about 21.8 cm for males and 22.8 cm for females. Possibly rex sole mature earlier in the southern portion of their range.

Spawning

Duration of the spawning period was from January through June, with a peak in March-April (Figure 7). Although samples were not obtained during August and December, the percentage of fish in each reproductive phase gives a good indication of the spawning time.

The 6-mo spawning period we found is longer than the January through April spawning reported by Villadolid (1927) for rex sole collected off central California in 1925 and 1926. Paul Reed (FCO, pers. commun.) found a prolonged spawning from January through August for 3,189 rex sole collected off northern California in 1949-54 and 1962-63. This suggests the duration of rex sole spawning varies by area and year.

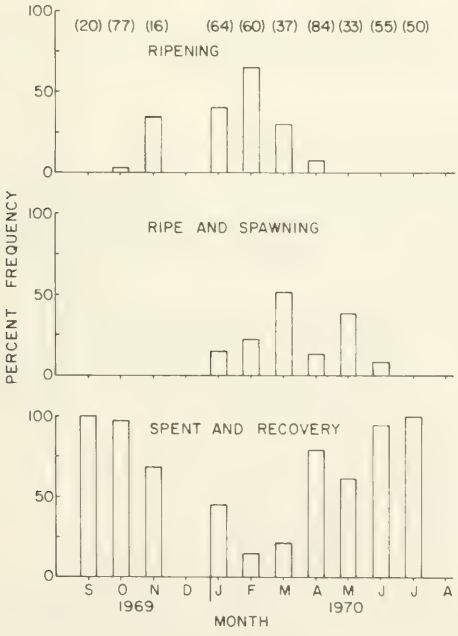

FIGURE 7.—Annual cycle of reproduction in 496 rex sole (274 males and 222 females) collected off northern Oregon, September 1969-July 1970. The number in each monthly sample is shown in parentheses.

Fecundity

Examination of 13 mature females ranging from 240 to 590 mm TL yielded fecundity estimates of 3,900 and 238,100 ova, respectively. The numbers of ova generally increased with size of the female. In 11 of 13 fish, the right ovary contained more ova than the left (100 to 12,700 more). A linear regression fitted to the fecundity-length data gave a correlation coefficient of 0.9620 (Figure 8). The formula for the regression line was $F = 5.3797 \times 10^{-7} L^{4.22667}$, where F is fecundity in number of ova and L is fish TL in millimeters.

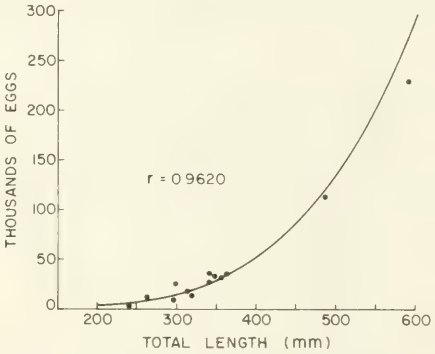

FIGURE 8.—Fecundity-length relationship for 13 rex sole collected off northern Oregon, February 1970.

Stock Identification

Tagging Experiment

A total of 2,537 rex sole were tagged and released off the northern Oregon coast in April (200) and June 1970 (2,337). There were 15 recaptures (0.59% recovery) by July 1974, all from the June 1970 tagging (Table 7). Maximum movement was 53.9 km, and 788 days was the longest time at liberty. There was little change in the depth range occupied by recaptured fish, which were released in 42-154 m and recovered by trawls in 51-101 m.

These results suggest only limited movement by rex sole. However, tag returns were too few to justify definite conclusions. This low recovery is similar to reports of rex sole tagged off British Columbia (Manzer 1952 [90 tagged]) and Oregon (Harry 1956 [19 tagged]) from which no fish were recovered.

TABLE 7.—Release and recovery data on 2,537 rex sole tagged off northern Oregon, April and June 1970.

Date	Number tagged	Number recovered	Percent recovery	Distance traveled (km)	Days at liberty
April 1970	200	0	0.00	0.0	0.0
June 1970	2,337	15	0.64	1.5	4
				17.1	4
				0.0	5
				3.7	18
				23.0	40
				14.1	189
				2.2	240
				8.0	278
				14.3	279
				0.9	294
				38.9	346
				53.9	364
				unknown	374
				3.9	450
				52.3	788
Total	2,537	15	0.59		

The low returns possibly were caused by rex sole not surviving the tagging process. Manzer (1952) reported rex sole reacted badly to capture and tagging. Most tagged rex sole released at the ocean surface did not immediately descend. Instead, unlike most other flatfish species, they curled into a semicircle and moved across the water surface in a skipping motion. This peculiar reaction might have resulted in a high initial tagging mortality from predation. It may also indicate a stress condition from which fish did not recover.

Starch-Gel Electrophoretic Analysis

There were 20 loci detected in the muscle tissue of 145 rex sole. Of these loci 13 were enzymes and 7 were muscle proteins (Table 8). Only three of the loci (15%) were polymorphic.

The polymorphism was found in only three of the eight systems studied or examined. AAT staining occurred in two anodal regions (A-I and A-II). Zone II was the only polymorphic region, having A, B, C, and D alleles (Figure 9, Table 9). The enzyme peptidase also had two anodal regions. Only zone II was polymorphic, with A and B alleles (Figure 10, Table 10). A third enzyme, PGM, was polymorphic, having only one locus which had A^1, A, and B alleles (Figure 11, Table 11).

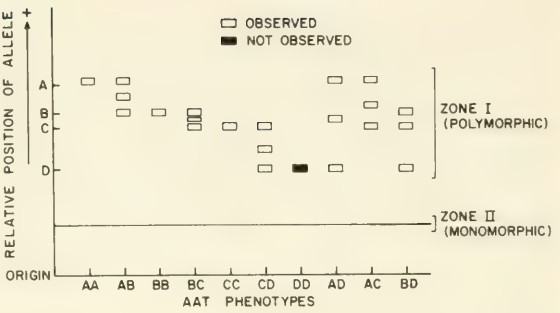

FIGURE 9.—Diagrammatic representation of aspartate aminotransferase (AAT) phenotypes in starch gel from 145 rex sole collected off Oregon, April 1973.

TABLE 9.—Frequencies of aspartate aminotransferase (AAT) phenotypes in 145 rex sole collected off Astoria, Charleston, and Brookings, Oreg., in April 1973.

Item	Astoria	Charleston	Brookings
Sample size	52	43	50
Date	5, 9 April	30 April	8 April
AAT phenotypes:			
AA	3	8	6
AB	18	3	10
BB	9	10	11
BC	12	12	9
CC	3	2	3
CD	1	0	0
DD	0	0	0
AD	1	1	0
AC	4	6	9
BD	1	1	2
Frequency of alleles:			
A	0.28	0.30	0.31
B	0.47	0.42	0.43
C	0.23	0.26	0.24
D	0.02	0.02	0.02

No discernible variation in the frequency or kinds of phenotypes found was observed between rex sole collections from off Astoria (northern),

TABLE 8.—Results of electrophoretic tests of muscle tissue samples from 145 rex sole collected off Oregon, April 1973.

Protein[1]	No. of bands in starch gel	Proposed no. of loci	Proposed no. of alleles per locus	Type of alleles found	Phenotypic variation
AAT A-I	1	1	1	—	Monomorphic
AAT A-II	4	1	4	A,B,C,D	Polymorphic
LDH	1	1	1	—	Monomorphic
Peptidase A-I	1	1	1	—	Monomorphic
Peptidase A-II	2	1	2	A,B	Polymorphic
PGM	3	1	3	A^1,A,B	Polymorphic
TO	1	1	1	—	Monomorphic
Muscle proteins[2]	7	7	1	—	Monomorphic

[1]AAT (aspartate aminotransferase); LDH (lactate dehydrogenase); PGM (phosphoglucomutase); TO (tetrazolium oxidase).
[2]Analysis of muscle proteins was nonspecific, with 6 anodal (+) bands and 1 cathodal (−) band found.

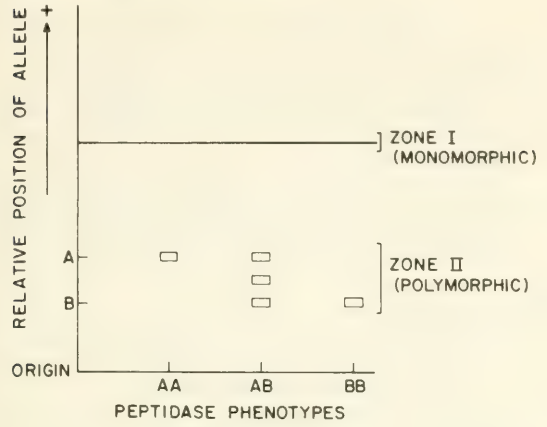

FIGURE 10.—Diagrammatic representation of peptidase phenotypes in starch gel from 137 rex sole collected off Oregon, April 1973.

TABLE 10.—Frequencies of peptidase anodal zone II phenotypes in 137 rex sole collected off Astoria, Charleston, and Brookings, Oreg., in April 1973.

Item	Astoria	Charleston	Brookings
Sample size[1]	50	43	44
Date	5, 9 April	30 April	8 April
Peptidase phenotypes:			
AA	10	10	13
AB	30	17	22
BB	10	16	9
Frequency of alleles:			
A	0.50	0.43	0.55
B	0.50	0.57	0.45

[1]An additional two rex sole from the Astoria sample and six fish from the Brookings sample did not develop distinct patterns and hence are not included.

Charleston (central), or Brookings (southern) Oregon (Tables 9-11). These data are insufficient to warrant extended speculation. However, they suggest that geographic selection or variation in rex sole off Oregon, if any, may not revolve around the genetic system included in the eight systems tested. Other alternatives, such as testing additional genetic systems or possible use of helminth parasites as biological tags, should be investigated to provide a more extensive evaluation of the population structure of rex sole off Oregon as a possible adjunct to effective management decisions.

ACKNOWLEDGMENTS

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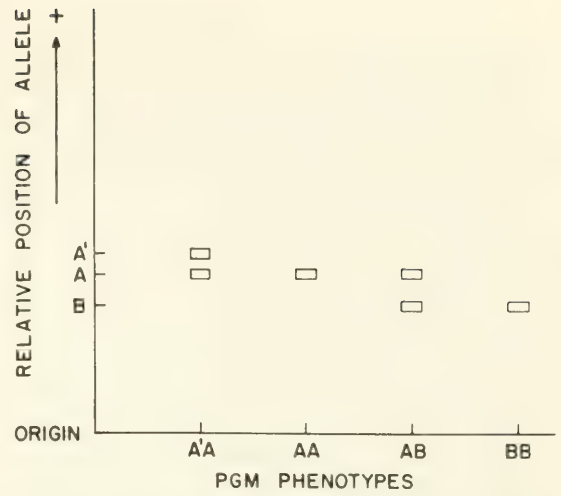

FIGURE 11.—Diagrammatic representation of phosphoglucomutase (PGM) phenotypes in starch gel from 145 rex sole collected off Oregon, April 1973.

TABLE 11.—Frequencies of phosphoglucomutase (PGM) phenotypes in 145 rex sole collected off Astoria, Charleston, and Brookings, Oreg., in April 1973.

Item	Astoria	Charleston	Brookings
Sample size	52	43	50
Date	5, 9 April	30 April	8 April
PGM phenotypes:			
A'A	0	0	1
AA	51	42	49
AB	0	1	0
BB	1	0	0
Frequency of alleles:			
A'	0.00	0.00	0.01
A	0.98	0.99	0.99
B	0.02	0.01	0.00

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ABUNDANCE AND POTENTIAL YIELD OF THE ROUND HERRING, *ETRUMEUS TERES*, AND ASPECTS OF ITS EARLY LIFE HISTORY IN THE EASTERN GULF OF MEXICO[1]

EDWARD D. HOUDE[2]

ABSTRACT

Eggs and larvae of the round herring, *Etrumeus teres*, were surveyed from plankton collections made in the eastern Gulf of Mexico from 1971 to 1974 to determine adult stock size, spawning areas, and spawning seasons and to study aspects of its early life history. Spawning occurred from mid-October through May where depths ranged from 30 to 200 m, surface temperatures from 18.4° to 26.9°C, and surface salinities from 34.5 to 36.5‰. A major spawning area was present 150 km from Tampa Bay between lat. 27°00′ and 28°00′N and long. 083°30′ and 084°30′W. Mean relative fecundity of 8 adult females was 296.5 ova per gram and the sex ratio of 71 adults was 1:1. The development time of eggs from spawning to hatching was approximately 2.0 days at 22°C. Three methods were used to determine adult biomass. The most probable annual estimates of biomass were approximately 700,000 metric tons in 1971-72 and 130,000 metric tons in 1972-73. The best estimates of the range of potential annual yields to a fishery were from 50,000 to 250,000 tons. Abundance and mortality rates of larvae were estimated in each year. It is probable that more than 99.4% mortality occurred between spawning and the 15.5-mm larval stage during 31 days in 1971-72 and more than 98.3% mortality occurred for the same period in 1972-73.

Round herring, *Etrumeus teres* (DeKay), is one of several clupeid fishes that are abundant in continental shelf waters of the eastern Gulf of Mexico. Distribution and abundance of this species was determined, based on egg and larvae surveys, as part of a program to investigate abundance and fishery potential for sardinelike fishes in the eastern Gulf. It is generally believed that several species of underexploited clupeid fishes from this area could provide significant catches (Bullis and Thompson 1967; Bullis and Carpenter 1968; Wise 1972) that would supplement yields of the heavily exploited Gulf menhaden, *Brevoortia patronus*. The egg and larvae surveys were carried out in 17 cruises from 1971 to 1974. Preliminary reports on clupeid abundance, based on these surveys, have been published (Houde 1973a, 1974) and overall results of the surveys were recently summarized (Houde 1976; Houde et al. 1976; Houde and Chitty 1976).

There are eight apparently discrete populations of *Etrumeus* in the world oceans. Whitehead (1963) has placed all of the forms in the single species *E. teres*. Recorded populations occur in the western Atlantic from Cape Cod into the Gulf of Mexico, in the eastern North Pacific from the Gulf of California to north of Los Angeles, in the central North Pacific near Hawaii, in the Indo-Pacific off the south and west coasts of Australia, in the western North Pacific off the coasts of Japan, in the western Indian Ocean off the east coast of South Africa, in the Red Sea, and near the Galapagos Islands in the Eastern Pacific.

Eggs and larvae of *E. teres* have been described from some areas where they occur (Blackburn 1941; Uchida et al. 1958; Mito 1961; Houde and Fore 1973; O'Toole and King 1974; Watson and Leis 1974). Ito (1968) examined fecundity and maturity of round herring from the Sea of Japan. Spawning by Hawaiian round herring recently was discussed by Watson and Leis (1974). Distribution and abundance of round herring eggs and larvae were reported in the Gulf of California (Moser et al. 1974; De la Campa de Guzman and Ortiz Jimenez 1975) and in the northern Gulf of Mexico by Fore (1971). Khromov (1969) found *Etrumeus* larvae to be common in plankton catches during a winter survey of the eastern Gulf of Mexico.

Round herring are fished commercially off Japan and South Africa. A catch of approximately 26,000 metric tons was made by South Africa in 1973 (Food and Agriculture Organization 1974;

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O'Toole and King 1974), and the Japanese catch was 40,400 metric tons in that year (Food and Agriculture Organization 1974). The species is not fished at present in the Gulf of Mexico. Salnikov (1969) reported that round herring was abundant in the northeastern Gulf of Mexico, and Harvey Bullis (pers. commun.) stated that it was plentiful in the eastern Gulf, based on acoustic traces and trawl catches made by National Marine Fisheries Service research vessels. Our initial surveys of eggs and larvae indicated that it might be abundant in the eastern Gulf (Houde 1973a), and Fore (1971) reported round herring eggs and larvae to be abundant in the northern Gulf of Mexico. In the absence of a commercial fishery, catch and effort statistics, and other data on abundance, I have estimated the adult biomass in the eastern Gulf from the abundance of eggs that were spawned annually. This fishery-independent technique of biomass estimation can provide preliminary knowledge of fishery potential (Ahlstrom 1968) and is considered to be a useful biomass estimating procedure (Saville 1964; Smith and Richardson in press).

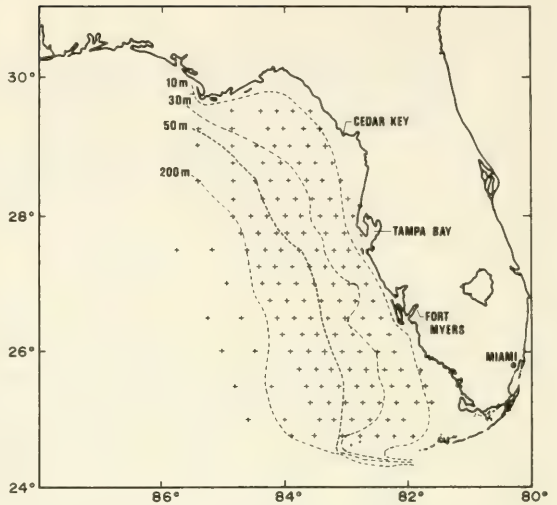

FIGURE 1.—Area emcompassed by the 1971-74 eastern Gulf of Mexico ichthyoplankton surveys. Plus symbols (+) represent stations that were sampled during the survey. The 10-, 30-, 50-, and 200-m depth contours are indicated.

METHODS

Survey Area and Times

Seventeen plankton surveys were made in the eastern Gulf of Mexico between lat. 24°45′ and 30°00′N (Figure 1) in 1971-74 (Table 1). Most sampling stations were located on the broad continental shelf, where depths ranged from 10 to 200 m, but a few stations were over the continental slope where depths were greater. Potential sampling stations were on transects running parallel to lines of latitude; transects were spaced at 15-nautical-mile (27.8-km) intervals. Stations were located at 15-mile (27.8-km) intervals on each transect, except for those stations beyond the 200-m depth contour, which were placed at 30-mile (55.6-km) intervals (Figure 1). Not all stations were sampled on each cruise (Table 1). Other details of survey planning and design have been reported elsewhere (Rinkel 1974; Houde et al. 1976; Houde and Chitty 1976).

Beginning with cruise IS 7205 (Table 1), sampling was restricted to stations on alternate transects. The three stations nearest to shore (at 27.8-km intervals) were sampled on each of the designated transects but only stations at 30-mile (55.6-km) intervals were sampled offshore. A few additional stations were added on 1974 cruises in areas where depth was less than 10 m; no round herring eggs or larvae occurred at these stations and they were not important with regard to spawning by this species, but they were important in determining spawning and distribution of other Gulf clupeids.

Plankton Sampling

A paired 61-cm Bongo net plankton sampler was used on all cruises except cruise GE 7101, in which a 1-m ICITA [International Cooperative Investigations of the Tropical Atlantic (Navy)] plankton net with 505-μm mesh was towed. Meshes on the Bongo sampler were 505 μm and 333 μm. Ichthyoplankton was sorted from the 505-μm mesh net and plankton volumes were determined from the 333-μm mesh net catch (Houde and Chitty 1976). Net tows were double oblique from within 5 m of bottom to surface or from 200-m depth to surface at deep stations. Nets were towed at approximately 3.0 knots (1.5 m/s) in 1971, but towing speed was reduced on later cruises and averaged 2.3 knots (1.2 m/s) (Table 2). Stations were sampled whenever the ship occupied them; thus, tows were made during either daylight or darkness, depending on the time of arrival at a station.

Prior to cruise GE 7208, all tows consisted of

TABLE 1.—Summarized data on cruises to the eastern Gulf of Mexico, 1971-74, to estimate abundance of round herring eggs and larvae. (GE = RV *Gerda*, 8C = RV *Dan Braman*, TI = RV *Tursiops*, 8B = RV *Bellows*, IS = RV *Columbus Iselin*, CL = RV *Calanus*.)

Cruise	Dates	Number of stations	Positive stations for eggs[1]	Positive stations for larvae[2]	Mean egg abundance under 10 m²		Mean larvae abundance under 10 m²	
					All stations	Positive stations	All stations	Positive stations
GE 7101[3]	1-8 Feb. 1971	20	4	9	39.37	196.88	7.34	16.30
8C 7113								
TI 7114	7-18 May 1971	123	2	24	0.21	12.88	3.00	15.80
GE 7117	26 June-4 July 1971	27	0	0	0.00	—	0.00	—
8C 7120								
TI 7121	7-25 Aug. 1971	146	0	0	0.00	—	0.00	—
TI 7131								
8B 7132								
GE 7127	7-16 Nov. 1971	66	15	20	41.41	187.73	4.18	14.20
8B 7201								
GE 7202	1-11 Feb. 1972	30	8	13	151.20	604.81	20.29	49.97
GE 7208	1-10 May 1972	30	2	2	1.38	22.11	0.28	4.44
GE 7210	12-18 June 1972	13	0	0	0.00	—	0.00	—
IS 7205	9-17 Sept. 1972	34	0	0	0.00	—	0.00	—
IS 7209	8-16 Nov. 1972	50	5	2	0.83	8.30	1.61	40.28
IS 7303	19-27 Jan. 1973	51	12	20	23.77	101.04	19.12	48.76
IS 7308	9-17 May 1973	49	2	3	2.48	60.72	2.29	37.41
IS 7311	27 June-6 July 1973	51	0	0	0.00	—	0.00	—
IS 7313	3-13 Aug. 1973	50	0	0	0.00	—	0.00	—
IS 7320	6-14 Nov. 1973	51	8	5	4.11	26.22	1.11	11.32
CL 7405[4]	28 Feb.-9 Mar. 1974	36	0	0	0.00	—	0.00	—
CL 7412	1-9 May 1974	44	1	1	0.49	21.50	3.98	175.07

[1]Positive station is a station at which round herring eggs were collected.
[2]Positive station is a station at which round herring larvae were collected.
[3]An ICITA, 1-m plankton net was used on this cruise. On all other cruises a 61-cm Bongo net was used.
[4]No stations in offshore areas were sampled, accounting for the failure to collect round herring eggs or larvae on this cruise.

TABLE 2.—Summary of plankton tow characteristics for 17 ichthyoplankton cruises to the eastern Gulf of Mexico. The 61-cm Bongo net sampler was used on all cruises except GE 7101 in which a 1-m ICITA net was used.

Cruises	Number of stations	Mean volume filtered (m^3)	Standard error of volume filtered (m^3)	Mean towing speed (m/s)	Standard error of towing speed (m/s)	Mean volume filtered per unit depth (m^3/m)	Standard error of volume filtered per unit depth (m^3/m)
GE 7101	20	675.25	30.29	—	—	49.69	11.58
8C 7113 & TI 7114 GE 7117 8C 7120 & TI 7121 8B 7132 & TI 7131 GE 7202 & 8B 7201	358	160.17	7.27	1.44	0.03	3.60	0.11
GE 7208 GE 7210 IS 7205 IS 7209 IS 7303 IS 7308 IS 7311 IS 7313 IS 7320	335 <55 m deep	104.39	0.92	1.17	0.01	11.04	0.57
CL 7405 CL 7412	124 >55 m deep	231.93	11.80	1.18	0.01	2.37	0.07

wire release at 50 m/min to desired depth and retrieval at 20 m/min. In later cruises, two types of tow were used, a shallow-water tow at stations less than 55 m deep and the usual 50 m/min release-20 m/min retrieval tow at deeper stations (Table 2). The shallow-water tow was of 5-min duration; it consisted of 1 min for wire release and 4 min for wire retrieval. The objective at shallow stations was to filter 100 m^3 of water. This objective was met, but the volume of water filtered per unit of depth fished by the net was increased significantly at the shallow stations relative to deeper stations (Table 2). This discrepancy in type of tow was considered to be more desirable than the alternative situation, which existed in 1971, when as little as 25 m^3 of water were filtered at some of the shallowest stations. Tows at stations deeper than 55 m filtered between 100 and 400 m^3.

A stopwatch was used to monitor each tow and the wire angle was measured at the end of each minute of a tow. A time-depth recorder gave a record of tow characteristics. Volume filtered was determined from a flowmeter in the mouth of the 505-μm mesh net.

Plankton Samples

All samples were preserved immediately in 10% seawater Formalin[3] buffered with marble chips. Samples were transferred to 5% buffered Formalin after they had been stored in the laboratory for 1 mo. Houde and Chitty (1976) have discussed methods used to determine plankton volumes. All fish eggs and larvae were sorted from each 505-μm mesh net plankton sample under a dissecting microscope for later identification and enumeration.

Eggs and larvae of round herring are distinctive and easily identified (Houde and Fore 1973). Round herring eggs from each station were enumerated; larvae were enumerated and measured with an ocular micrometer in a dissecting microscope.

Temperatures and Salinities

Temperature and salinity profiles of the water column at each station were obtained on all cruises.[4] Usually a mechanical bathythermograph cast was made to describe the vertical temperature profile. This was followed by a hydrocast consisting of from two to seven 1.7-liter Niskin bottles with reversing thermometers. Samples for salinity were brought to Rosenstiel School of Marine and Atmospheric Science for analysis. On cruises IS 7308 and IS 7320 a salinity-temperature depth unit was used in place of the Niskin bottles to obtain temperature and salinity data. Round herring egg and larva data were examined in relation to temperatures and salinities at stations where they were collected.

Determining Egg and Larvae Abundance

Catches of round herring eggs and larvae at each station were standardized to give abundance in numbers under 10 m^2 of sea surface:

$$n_j = \frac{c_j z_j}{v_j} \cdot 10 \qquad (1)$$

where n_j = the number of individuals (eggs or larvae) at station j under 10 m^2 of sea surface

c_j = the catch of eggs or larvae at station j

z_j = the depth of tow (in meters) at station j

v_j = the volume filtered by the net (in cubic meters) at station j.

Both total larval abundance under 10 m^2 and larval abundance in each 1.0-mm length class under 10 m^2 were determined.

Numbers of eggs or larvae also were estimated in the area represented by each station. These areas were determined by the polygons described by the perpendicular bisectors of lines from the station in question to adjacent stations (Sette and Ahlstrom 1948):

$$p_j = \frac{c_j z_j}{v_j} \cdot A_j \qquad (2)$$

where p_j = the estimated total number of eggs or larvae in the area represented by station j

c_j, z_j, and v_j are defined in Equation (1)

A_j = the area (in square meters) represented by station j.

Total larvae and larvae by 1.0-mm length classes were estimated for each station area. Most stations represented areas ranging from 0.75 to 3.15 $\times$ 10^9 m^2.

The estimated total number of eggs and larvae, as well as larvae by 1.0-mm length classes, was estimated for the entire area represented by each cruise:

$$P_{i.} = \sum_{j=1}^{k} p_j \qquad (3)$$

where $P_{i.}$ = the cruise estimate (i.e., the total number of eggs or larvae estimated in the area represented by cruise i)

k = the number of stations sampled during cruise i

p_j is defined by Equation (2).

Variance estimates on the abundance of eggs were obtained for each cruise using a combination of methods outlined by Cushing (1957) and Taft (1960). Only stations at which round herring eggs had been collected at least once during the 1971-74 survey period were included in obtaining these estimates. Other stations were considered to be outside the area of spawning, because round herring eggs were never collected there. These usually were the three stations on each transect that

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4]Temperature and salinity data for these cruises can be retrieved from the MAFLA file at the National Oceanographic Data Center, Washington, D.C.

were located closest to the coast (Figure 1). An estimate of the variance in egg abundance under a square meter of sea surface (s_{ij}^2) was obtained from the $\log_{10}((c_j z_j)/v_j) + 0.1$ egg catch at each station during a cruise (Cushing 1957). The $\log_{10}$ variance estimate so obtained was backtransformed to obtain the untransformed estimate of variance. The variance estimate for a cruise was calculated using the estimator given by Taft (1960) that assumes random sampling. It is:

$$S_{P_i}^2 = D_i^2 \sum_{j=1}^{k_i} \frac{A_{ij}^2 s_{ij}^2}{d_{ij}^2} \qquad (4)$$

where $S_{P_i}^2$ = variance estimate on the abundance of eggs spawned during the period represented by cruise i

D_i = the number of days represented by cruise i, defined as the days included in the cruise plus one-half the days since the previous cruise and one-half the days to the next cruise (Sette and Ahlstrom 1948). When a cruise took place shortly after the assumed date of the beginning of the round herring spawning period (15 October) or near the end of the spawning season (31 May), the number of days from the inclusive cruise days to the beginning or end of the season was used in estimating D_i

A_{ij} = the area (m^2) represented by the jth station in the ith cruise

d_{ij} = the duration (days) of the egg stage from spawning until hatching. The best estimate of d_{ij} for round herring is 2.0 days, based on observed egg stages in catches during the surveys and this value was used in all abundance and variance calculations

s_{ij}^2 = the variance estimate for the number of eggs present under 1 m^2 of sea surface for cruise i

k_i = the number of stations included in the variance estimate for cruise i.

Sampling was not random in the eastern Gulf surveys. Also, egg catches were not normally or log-normally distributed, nor did the distribution of catches fit contagious distributions like the negative binomial. Thus, the variance estimates that I have obtained are not the best estimates, but they may be reasonable approximations (Saville 1964) for variance in the area represented by the cruises. Variation in spawning that occurs over time (i.e., day to day variation) has not been accounted for, which is the usual situation in ichthyoplankton abundance surveys (Saville 1964).

An estimate of the abundance of eggs spawned over the entire spawning season is:

$$P_a = \sum_{i=1}^{r} \frac{P_i D_i}{d_i} \qquad (5)$$

where P_a = the total number of eggs spawned in an annual spawning season

r = the number of cruises upon which the estimate of annual spawning is based

P_i, D_i, and d_i are defined in Equation (4).

An estimate of variance on the number of eggs spawned annually was obtained, assuming that sampling was random using the formula given by Taft (1960):

$$S_{P_a}^2 = \sum_{i=1}^{r} S_{P_i}^2 \qquad (6)$$

where $S_{P_a}^2$ = the variance estimate on the number of eggs spawned annually

r is defined in Equation (5)

$S_{P_i}^2$ is defined in Equation (4).

This variance estimate, like that for individual cruise abundance estimates, is not entirely satisfactory because the assumptions of random sampling and normally distributed catches do not hold. Also, as in the cruise variance estimates (Equation (4)), it was not possible to obtain an estimate of variance in abundance due to day to day variability, thus leaving variation in time unaccounted. Taft has shown that this can be a large source of error and that annual spawning estimates will not be more precise than individual cruise estimates when variation in time is not considered.

Biomass Estimating Procedure

An estimate of adult biomass of a fish stock can be obtained if the annual spawning (number of eggs), sex ratio, and relative fecundity (eggs produced per gram adult female per year) are known (Saville 1964; Ahlstrom 1968). Biomass of adults is:

$$B = \frac{P_a}{F_r \cdot K} \quad (7)$$

where B = biomass of adults in the stock
F_r = mean relative fecundity of females (eggs produced per gram female per year)
K = the proportion of adults that are females
P_a is defined in Equation (5).

Estimates of P_a, F_r, and K were obtained for round herring in the Gulf of Mexico.

An estimate of K was derived from examination of 71 gonads of adult round herring trawled from the Gulf of Mexico by the National Marine Fisheries Service. The estimate of F_r also was obtained from these specimens. Fecundity was estimated by the gravimetric method (Holden and Raitt 1974). Modes of yolked oocytes were assumed to be spawned during an annual spawning cycle. This assumption was supported by the presence of only a single mode of unyolked oocytes in six females collected during months when no spawned eggs were collected in plankton tows. Fecundity was estimated in a sample of eight near-ripe females. Procedures used to estimate round herring fecundity are like those outlined for scaled sardine, *Harengula jaguana,* by Martinez and Houde (1975).

Three techniques were used to estimate adult biomass. All give estimates of annual spawning (P_a) that are based on the same egg catches, standardized per unit area of sea surface. Thus, the three estimates of biomass for each spawning season are not independent; but, because each technique has unique assumptions, the spawning estimates are different, and it was useful to calculate biomass by each procedure for comparison purposes. The three techniques are outlined by Sette and Ahlstrom (1948), Simpson (1959), and Saville (1956, 1964).

The method first used by Sette and Ahlstrom (1948) and subsequently by Ahlstrom (1954, 1959a) is based on obtaining an estimate of annual spawning by the techniques that I have outlined in Equations (2), (3), (5), and (7). It assumes that the abundance of eggs at a station is equal over the entire area represented by that station. Moreover, it assumes that egg abundance at the time of collection is the same on each day of the cruise period and also for one-half the days since the preceding cruise, or since the beginning date of the spawning season plus one-half the days until the next cruise or the number of days until the end of the spawning season.

Simpson's (1959) method was modified to obtain round herring annual spawning estimates. He obtained his estimates of spawning during each cruise by summing areas within contours of egg abundance. I used Equation (3) to obtain cruise estimates. The annual spawning estimate (P_a) was obtained by plotting the daily spawning estimate for each cruise (P_i/d_i) against the middate of the cruise (Simpson 1959). The area under the resulting polygon was obtained by planimeter and was equated to annual spawning. Because Equation (3) was used to obtain cruise spawning estimates, Sette and Ahlstrom's (1948) and Simpson's (1959) methods give results that converge, the two annual spawning estimates differing only by some number of eggs spawned near the beginning and near the end of the spawning season. The Sette and Ahlstrom technique will always give a somewhat larger estimate of annual spawning for species like round herring that have a well-defined spawning season, but identical estimates will result for species that spawn year round.

The third method (Saville 1956, 1964) assumes that spawning follows some known distribution during the season. Spawning is approximately normally distributed throughout the season for many fishes. Thus, cruises that fall within the spawning season represent part of the area under the normal curve. If the peak spawning date is known (even approximately) each cruise can be equated to some percentage of the area under a standard normal curve. Then each cruise spawning estimate (P_i) can be used to obtain an annual spawning estimate (P_a):

$$\frac{P_i \cdot t_i}{x_i d_i} = P_a \quad (8)$$

where x_i = the proportion of the area under the normal curve represented by cruise i
t_i = the number of days included in cruise i
d_i = the duration (days) of the egg stage during cruise i.

Saville (1956, 1964) did not discuss use of the technique if more than a single cruise is included in the spawning season, but because each cruise can provide an independent estimate of annual spawning, it was possible to get as many as three estimates of round herring annual egg production within a spawning season.

Potential Yield to a Fishery

Alverson and Pereyra (1969) and Gulland (1971, 1972) have proposed that an estimate of potential yield for an unfished stock can be obtained if the virgin biomass and natural mortality coefficient are known. The estimator is:

$$C_{max} = XMB_0 \quad (9)$$

where C_{max} = the maximum sustainable yield
X = a constant, assumed to be 0.5 (Gulland 1971).
M = the natural mortality coefficient. It is equal to Z, the total mortality coefficient, in an unfished stock.
B_0 = the virgin biomass. My biomass estimates of round herring are estimates of B_0 because there is no significant fishing at this time.

No estimates of M are available for round herring. It seems probable that it must lie in the range 0.4-1.0, based on literature on other relatively short-lived tropical and warm temperate clupeid stocks (Beverton 1963; Schaaf and Huntsman 1972; Dryfoos et al. 1973) and from the empirical relationship of M to life span given by Tanaka (1960). Assuming M is between 0.4 and 1.0, a range of potential yields to a fishery can be predicted. I used this approach for round herring.

Larval Abundance and Mortality

As a first step in determining survival rates of round herring larvae for comparisons among years and to determine abundance of larvae by length classes, larval abundance was estimated for each 1-mm length class:

$$P_{al} = \sum_{i=1}^{r} D_i \sum_{j=1}^{k} \frac{c_{jl} z_j}{v_j} \cdot A_j \quad (10)$$

where P_{al} = the annual estimate of total larvae in a length class l; this is the estimate if no correction is made for night-day variation in catches
c_{jl} = the catch of larvae in length class l at station j on cruise i
z_j = the depth of tow (in meters) at station j on cruise i
v_j = the volume filtered (in cubic meters) at station j on cruise i
A_j = the area (in square meters) represented by station j on cruise i
k = the number of stations sampled during cruise i
D_i = the number of days represented by cruise i (for details, see definition under Equation (4))
r = the number of cruises upon which the estimate is based.

Larval abundance estimates are subject to errors due to escapement of small larvae through the meshes and due to avoidance of the gear by larger larvae (Smith and Richardson in press). Avoidance usually is greater during daylight than at night. Some of the avoidance error can be corrected if the differential between night and day catches of larvae in each length class is evaluated. Catches of round herring larvae were examined from each station for 1971-73 cruises. The ratios of the sum of larvae estimated under 10 m² of sea surface caught at night stations to the sum of larvae estimated under 10 m² of sea surface caught at day stations were determined for each 1-mm length class. These ratios were then used to derive functions that corrected the day-caught larval abundance estimates. Thus, abundance of larvae in each 1-mm length class at stations occupied during daylight was corrected by a factor R:

$$P_{jl} = \frac{c_{jl} z_j}{v_j} R \cdot A_j \quad (11)$$

where P_{jl} = the number of larvae in length class l in the area represented by station j
R = the factor by which the number of larvae in length class l at station j should be multiplied to correct for night-day variation. It equals 1.0 for stations sampled at night.
c_{jl}, z_j, v_j, and A_j are defined in Equation (10).

R is greater than 1.0 if avoidance is more pronounced during daylight hours. The corrected station catches (from Equation (11)) were substituted into Equation (10) for larvae caught at stations occupied during daylight. Corrected larvae abundance estimates (P_{al}) were then obtained.

Larval mortality rates can be determined and expressed in terms of age if the growth rate of larvae is known or if a model of growth during the larval stage can be used to describe growth adequately. Smith and Richardson (in press)

recently have discussed the problem of obtaining crude mortality rates of larval fishes. A range of possible mortality estimates for round herring egg and larvae stages has been obtained which is useful for year to year comparisons and for comparison with larval mortality estimates that have been published on other species. Growth rates of round herring larvae are unknown and could not be determined from the data. But, from my experience in laboratory culture of clupeid larvae, an exponential model describes growth reasonably well during the larval stage. Ahlstrom (1954) and Nakai and Hattori (1962) assumed that exponential growth was valid in determining survival rates of California sardine, *Sardinops caeruleus,* and Japanese sardine, *S. melanosticta,* larvae. From laboratory rearing experiments it is evident that mean daily growth increments ($\bar{b}$) of clupeid larvae range from 0.3 to 1.0 mm (Houde 1973b), the increments depending on such factors as temperature and food concentration. Using this basic information, the probable mortality rates of round herring larvae from hatching until 16.0 mm SL (standard length) were estimated for the 1971-72 and 1972-73 spawning seasons.

Using a computer program several variables were considered and then the instantaneous mortality coefficient was calculated for larvae based on predetermined combinations of values of the variables. The following procedure was used:

1) For each designated mean daily growth increment ($\bar{b}$), an instantaneous growth coefficient (g) is calculated.

a)
$$t = \frac{L_t - L_0}{\bar{b}} \qquad (12)$$

where t = the time in days to grow from L_0 to L_t at a mean daily growth increment $\bar{b}$
L_t = the maximum length of larvae considered to adhere to the exponential growth model (usually 20.0 mm SL)
L_0 = the minimum length of larvae to be considered in calculating the instantaneous growth coefficient (g). (This value was 4.1 mm SL for round herring.)

b)
$$g = \frac{\log_e L_t - \log_e L_0}{t} \qquad (13)$$

where g = the instantaneous growth coefficient. A different value of g results from each value of $\bar{b}$ that is submitted to the program.

2) The annual spawning estimate (P_a) for a given spawning season and the larval abundance estimates by 1-mm length classes, corrected for night-day variation (P_{al}) are entered.
3) The duration (in days) of each class from 2) above is determined:
   a) The egg: Duration is arbitrarily assigned, based on knowledge of developmental stages in plankton collections or from laboratory rearing experiments. For round herring in the eastern Gulf of Mexico it is 2.0 days.
   b) Nonfully vulnerable length classes: Duration is arbitrarily assigned, usually by submitting a range of possible values in the program. Larvae in these length classes are underrepresented in catches because of escapement through the meshes, and are not considered in subsequent mortality estimation.
   c) Fully vulnerable length classes.

$$D_t = \frac{\log_e L_B - \log_e L_A}{g} \qquad (14)$$

where D_t = duration of the class (in days)
L_B = upper boundary of length of a size class
L_A = lower boundary of length of a size class
g is defined in Equation (13).

4) The mean age of each class is then estimated:
   a) The egg: Mean age is arbitrarily assigned. (It is one-half the assigned duration.)
   b) Nonfully vulnerable length classes: Mean age is assigned. It equals duration of the egg stage plus one-half the duration of nonfully vulnerable length classes.
   c) The mean age of fully vulnerable length classes.

$$T_A = \text{duration of the egg stage} + \text{duration of nonfully vulnerable length classes} + \frac{\log_e L_b - \log_e L_a}{g} \qquad (15)$$

where L_b = the midpoint of the length class under consideration
L_a = the smallest length larva considered to be fully vulnerable to the gear
g is defined in Equation (13).

5) Abundance estimates for each class are corrected for duration. This is necessary to estimate the number present at mean age in that class. If exponential growth holds, the number of larvae in each successive age group will have been underestimated before the duration correction was made, because the time spent by larvae in successive length classes is decreasing. The correction is made by dividing the abundance estimates of each class (including the egg stage) from step 2 above by their durations, given in step 3.

6) The instantaneous mortality coefficient is then calculated for each combination of mean daily growth increment, assigned egg stage duration, and assigned nonfully vulnerable larvae duration. It is estimated from the exponential regression of night-day-corrected and duration-corrected abundances on mean age and is fitted for all age-classes that were adequately represented in the data, excluding nonfully vulnerable larvae. For round herring the regression was fit for age-classes including the egg stage and larvae ranging from 4.1 to 16.0 mm SL.

$$N_t = N_0 \exp(-Zt) \qquad (16)$$

where Z = the instantaneous coefficient of rate of decline in catch. It is the instantaneous mortality coefficient if factors such as gear avoidance are not significant contributors to the decline in catch as larvae grow older

N_t = the number of eggs or larvae at time t

N_0 = the y-axis intercept; it is an estimate of abundance at time 0 (i.e., the number of eggs that was spawned)

t = the time (in days) from spawning.

7) Mortality with respect to length also is estimated in the exponential regression of night-day-corrected abundance on length. Only fully vulnerable length classes were used in this calculation. For round herring, larvae from 4.1 to 16.0 mm SL were included in the analysis.

$$N_L = N_A \exp(-ZL) \qquad (17)$$

where Z = the instantaneous coefficient of rate of decline in catch. It is the instantaneous mortality coefficient per millimeter of standard length if factors such as gear avoidance do not contribute significantly to decline in catch as larvae grow.

N_L = the number of larvae of length L

N_A = the y-axis intercept

L = the standard length (millimeters) of larvae.

RESULTS

Occurrence of Eggs and Larvae

Eggs and larvae of round herring were collected on cruises from November to May (Table 1), and were most common in January and February. They did not occur in cruises from June through September, indicating that there is no spawning during summer in the eastern Gulf of Mexico. Most eggs and larvae were collected on the outer continental shelf (Figure 2) where depths ranged from 30 to 200 m. Eggs occurred on only two occasions at stations less than 30 m deep and on a single occasion at a station deeper than 200 m (Figure 2), although relatively little sampling effort was made at stations beyond the 200-m depth contour. Occurrences of larvae were more widespread (Figure 2), as expected due to dispersal by water currents, but most occurrences remained within the 30- to 200-m depth zone. The observed distribution suggests that most of the adult population is found on the outer shelf, at least during the spawning season. A major spawning center is located between long. 082°30′ and 084°30′W and lat. 27°00′ and 28°00′N (Figures 2-6). The location is about 150 km from Tampa Bay in a west by southwest direction. This is the same general area where round herring adults were trawled in exploratory fishing surveys (Anonymous 1958; Salnikov 1969). There is evidence that a second minor spawning center is found between long. 082°00′ and 083°30′W and lat. 24°45′ and 25°30′N. This location is just north of the Dry Tortugas Islands.

The cruise means for numbers of round herring eggs under 10 m² ranged from 0.00 to 151.20 for the 17 cruises in the survey (Table 1). Considering only positive stations (i.e., stations where round herring eggs were collected on a cruise), cruise means ranged from 8.30 to 604.81 under 10 m² of sea surface (Table 1). Catches at individual stations frequently ranged from 11 to 1,000 under 10 m² but exceeded 1,000 on only three occasions during the 17 cruises (Figures 3-6). Round herring

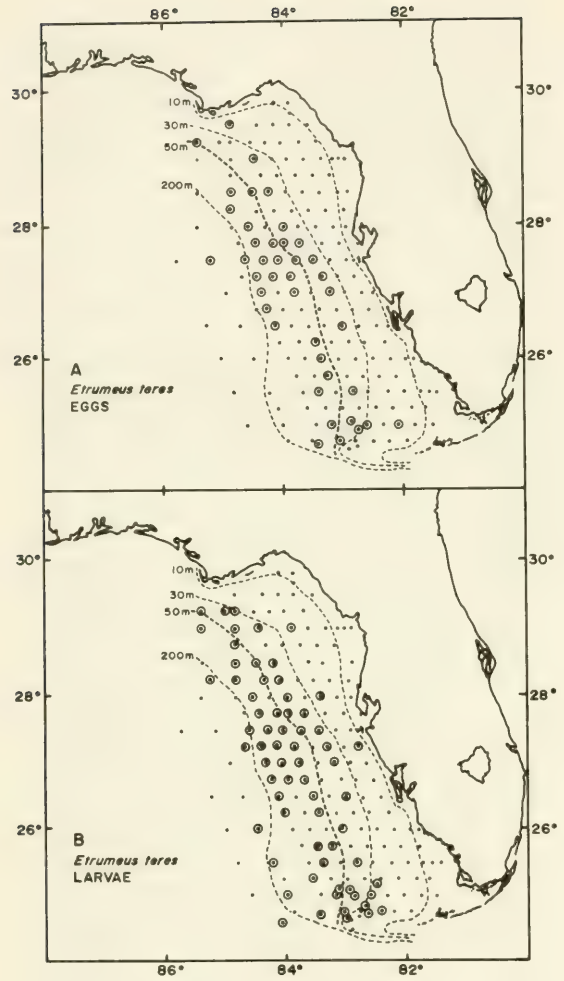

FIGURE 2.—A.) Stations in the survey area where eggs of round herring were collected at least once during 1971-74. Stations where eggs did not occur are indicated by dots. B). Stations in the survey area where larvae of round herring were collected at least once during 1971-74. Stations where larvae did not occur are indicated by dots.

egg abundances for each cruise at all stations, as well as summaries for other clupeid species, have recently been reported (Houde et al. 1976).

Cruise means for round herring larvae ranged from 0.00 to 20.29 under 10 m^2 (Table 1). At positive stations the cruise means for larvae ranged from 4.44 to 175.07 under 10 m^2 (Table 1), but the latter value was based on a single positive station for cruise CL 7412. Excluding that cruise, the highest mean larval abundance under 10 m^2 at positive stations was 49.97. No stations had more than 1,000 larvae under 10 m^2 during the 17 cruises. Tabulated station data on catches and abundance of round herring, and other clupeid larvae, have been published (Houde et al. 1976).

The survey area did not encompass the entire spawning area of round herring in the eastern Gulf. Eggs were collected at stations located farthest offshore on some cruises (Figures 3-6) but abundance was less at stations deeper than 200 m than at shallower stations. I believe that most of the spawning area and spawning population was included in the survey area, and that my egg abundance estimates suffer only small biases because of failure to sample a part of the population.

There was no apparent difference in the intensity of round herring spawning at stations between 30 and 50 m deep compared with stations deeper than 50 m. The $\log_{10}$ mean abundance estimates of eggs under 10 m^2 of sea surface for all positive stations $\leq$50 m and for those >50 m were calculated from pooled data of all cruises that had round herring eggs. The $\leq$50 m $\log_{10}$ mean was 1.6351 ($n = 25, S_{\bar{x}} = 0.1609$); the >50 m $\log_{10}$ mean was 1.5585 ($n = 32, S_{\bar{x}} = 0.1209$). These means did not differ significantly (t-test; $P > 0.50$). However, the area between the 30- and 50-m depth contours was less than that included between the 50- and 200-m contours. The total area between the 30- and 200-m depth contours was considered to be the spawning area; 40.1% of the area is in the 30- to 50-m zone while 59.9% is between 50 and 200 m. Thus, the total abundance of eggs in the area where depths exceeded 50 m probably was greater than abundance in shallower areas. The 50-m depth contour divides the shelf area in the eastern Gulf into approximate halves. For eight cruises in which sampling effort was distributed nearly equally to include potential spawning area in water $\leq$50 m and >50 m (cruises 8C 7113-TI 7114, 8B 7132-TI 7131-GE7127, 8B 7201-GE 7202, GE 7208, IS 7209, IS 7303, IS 7308, and IS 7320), the summed totals of egg abundance from the areas represented by stations on these cruises were compared with respect to the 50-m depth contour. A total abundance of 11.92×10^{11} eggs was estimated for stations $\leq$50 m; total abundance was 16.73×10^{11} at deeper stations. If these egg abundance estimates reflect relative adult abundance, then 41.6% of the adult population was located in depths $\leq$50 m and 58.4% was distributed at depths >50 m. The total abundance of eggs, and apparently of adult round herring, is directly proportional to the surface area of the two depth zones. Some small fraction of the spawning population inhabited depths greater than those sampled in

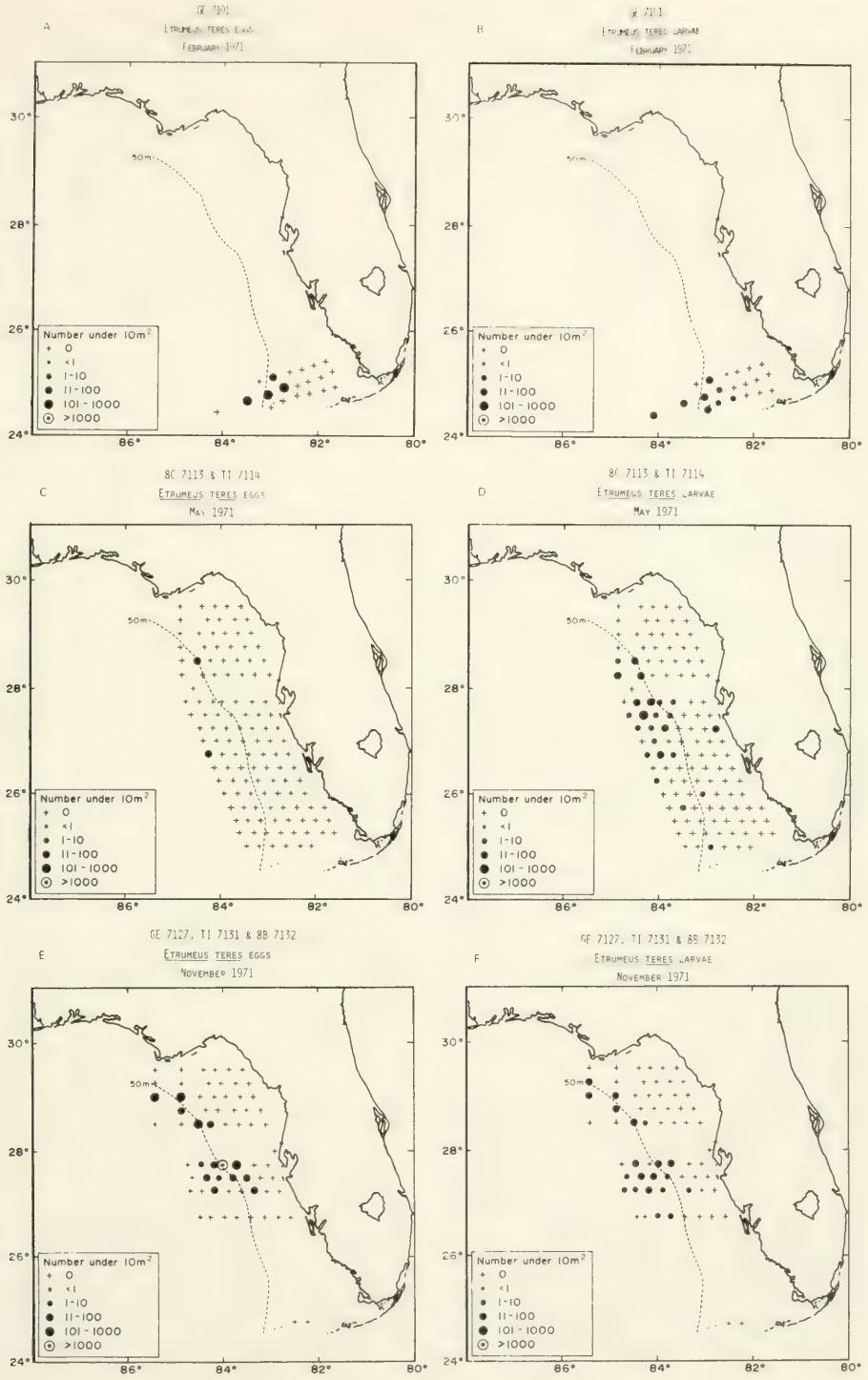

FIGURE 3.—Distribution and abundance of round herring eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B: Cruise GE 7101, February 1971. C, D: Cruise 8C 7113-TI 7114, May 1971. E, F: Cruise GE 7127-TI 7131-8B 7132, November 1971.

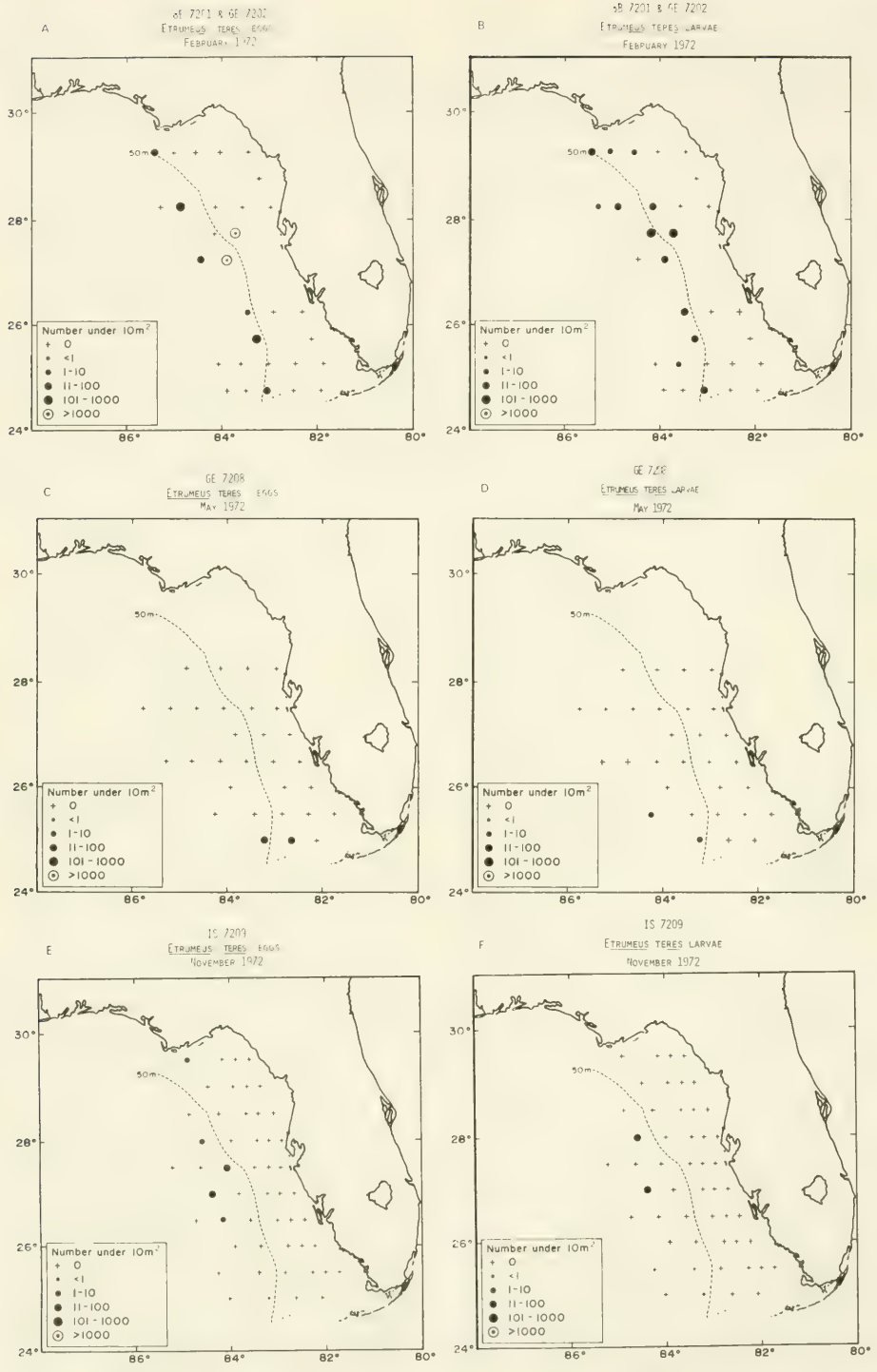

FIGURE 4.—Distribution and abundance of round herring eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B: Cruise 8B 7201-GE 7202, February 1972. C, D: Cruise GE 7208, May 1972. E, F: Cruise IS 7209, November 1972.

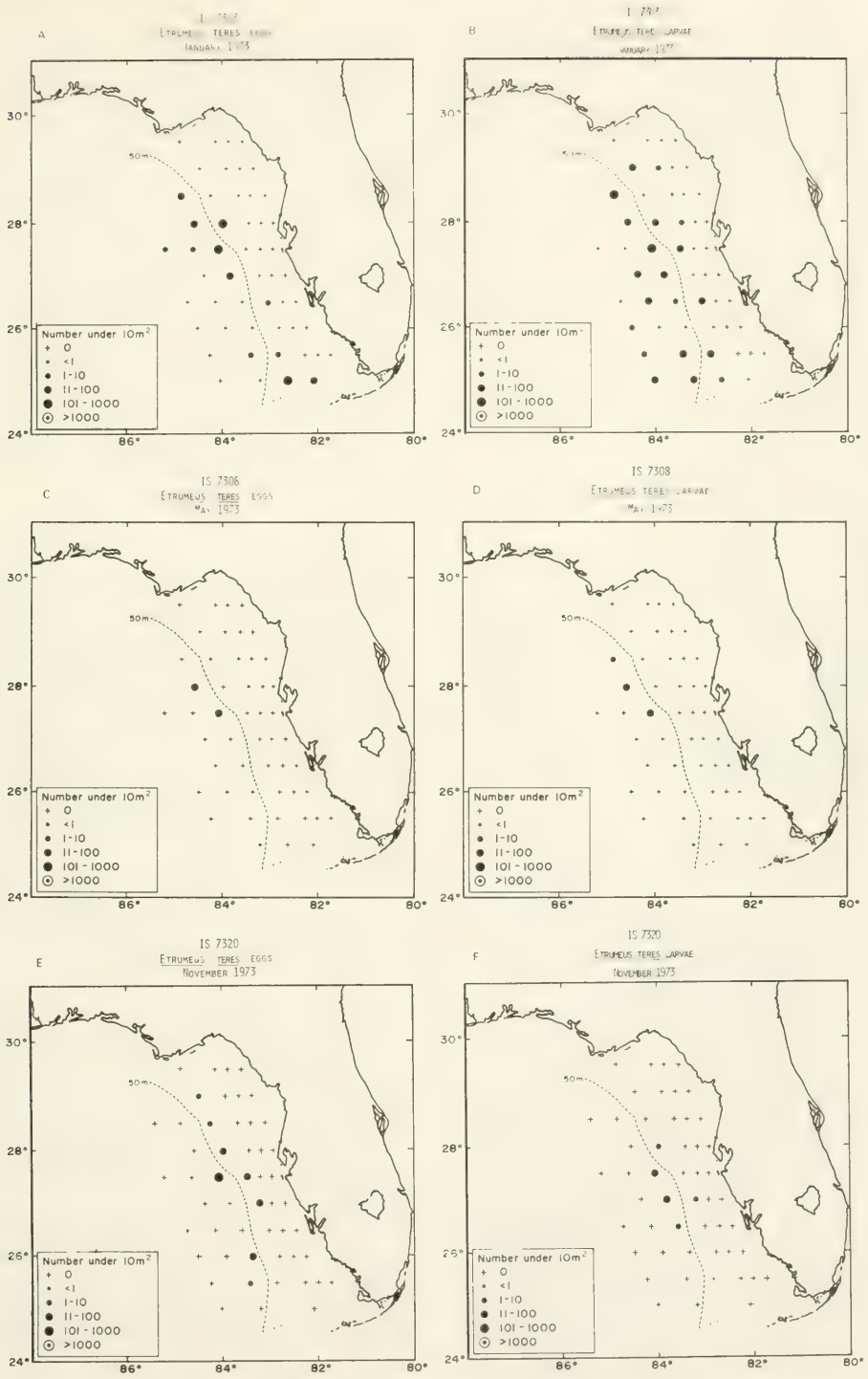

FIGURE 5.—Distribution and abundance of round herring eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B: Cruise IS 7303, January 1973. C, D: Cruise IS 7308, May 1973. E, F: Cruise IS 7320, November 1973.

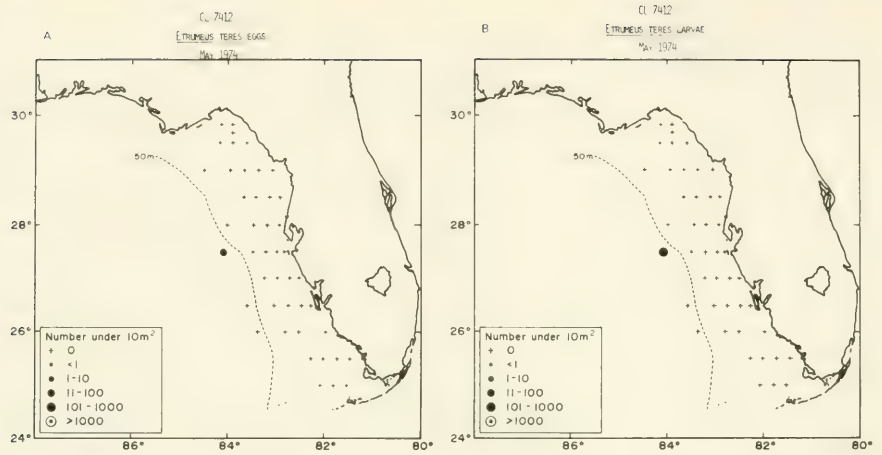

FIGURE 6.—Distribution and abundance of round herring eggs and larvae on cruise CL 7412, May 1974. Catches are standardized to numbers under 10 m^2 of sea surface.

our survey and the relative abundance of adults in water >50 m deep may be higher than the estimated 58.4%. Because the intensity of spawning was the same in depths, ≤50 and >50 m, adults apparently are not more abundant per unit of sea surface in deeper water but their greater abundance reflects the larger area of habitat suitable for round herring where shelf waters are >50 m deep.

Temperature and Salinity Relationships

Round herring eggs were collected when surface temperatures ranged from 18.4° to 26.9°C. They occurred at surface salinities of 34.50-36.50‰. Because no vertically stratified tows of the Bongo sampler were made, the percentage of eggs or larvae that occurred in surface waters is unknown. Surface temperatures from November to May were 0°-3°C higher than those at 50 m when vertical sections along transects at three latitudes were examined for each cruise in which round herring eggs or larvae were collected. Surface salinities differed by less than 0.5‰ from those at 50-m depth, except on cruise IS 7320 when surface salinities ranged from 0.6 to 1.0‰ less than those at 50 m. It is reasonable to believe that surface temperatures and salinities are representative of conditions where pelagic eggs were incubated and where larvae were found. Salinity may not be an important factor affecting spawning since the range of surface salinities at which eggs were collected nearly encompasses the entire range of salinities found in offshore waters of the eastern Gulf. Larvae ≤5.0 mm SL are from 0 to about 6 days old. They occurred where surface temperatures ranged from 20.5° to 26.9°C and surface salinities from 34.10 to 36.80‰.

The percentage cumulative frequency distributions (Figure 7) of stations where eggs or ≤5.0-mm larvae occurred in relation to temperature and salinity were examined. For eggs, 82.5% of the occurrences were between 21° and 26°C surface temperature, while 87.2% of the ≤5.0-mm larvae occurrences were in that temperature range. Only 10.5% of the egg occurrences were at stations where surface temperatures exceeded 26°C and only 6.4% of the ≤5.0-mm larvae occurrences were at such stations. The distribution of egg occurrences in relation to temperature was similar in the 1971-72 and 1972-73 spawning seasons. In 1971-72, 78.3% of the eggs occurred at stations where surface temperatures were less than 25°C; in 1972-73, 79.0% of the occurrences were at temperatures below 25°C. Comparable data were not available for the 1973-74 spawning season.

More than 50% of round herring eggs and ≤5.0-mm larvae were collected at stations where surface salinity exceeded 36.00‰ (Figure 7). For eggs, considering all years' data, 79.7% of the occurrences were at surface salinities from 35.50 to 36.50‰; for ≤5.0-mm larvae, 80.0% of the occurrences were in that salinity range. In 1971-72, 88.0% of the egg occurrences were at stations with surface salinities from 35.50 to 36.50‰; in 1972-

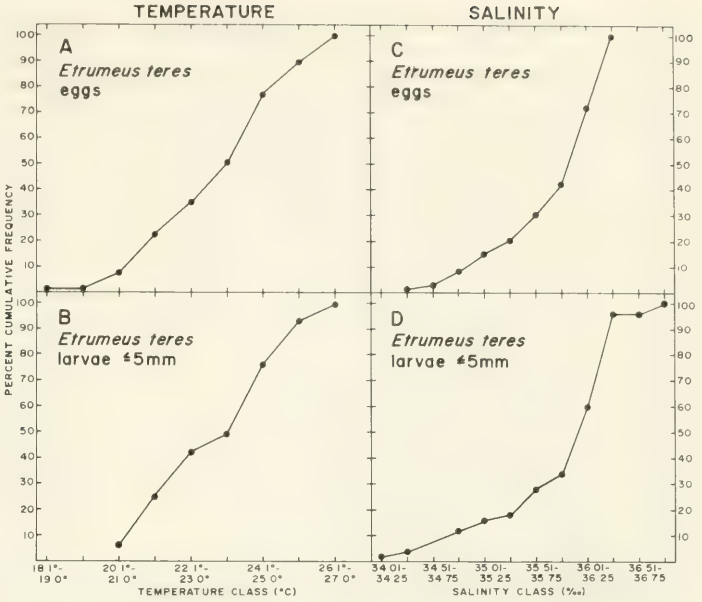

FIGURE 7.—Percent cumulative frequency distribution of 1971-74 stations where round herring eggs occurred in relation to surface temperatures (A) and to surface salinity (C), and ≤5.0-mm SL larvae occurred in relation to surface temperature (B) and surface salinity (D).

73, 94.7% of the egg occurrences were in that salinity range. There were seven egg occurrences at less than 35.50‰ surface salinity on cruise IS 7320 (November 1973). This cruise influenced the cumulative frequency distribution of egg occurrences in relation to salinity (Figure 7) over all years. Data for the entire 1973-74 spawning season were not available to compare occurrence of eggs in relation to salinity with 1971-72 and 1972-73 data; but, the frequency distribution apparently would have been shifted to lower salinities in that year, reflecting low surface salinities that prevailed in the eastern Gulf in fall 1973.

Egg and Larvae Abundance in Relation to Zooplankton

There was no apparent relationship between zooplankton volumes and round herring egg or larvae abundance. Zooplankton volumes (cubic centimeters/1,000 m^3 strained) were determined at each station for cruises in 1972 through 1974. Round herring egg abundance and larvae abundance were examined in relation to zooplankton volume for stations included in those cruises but the correlations were not significant.

Fecundity and Maturity

A total of 71 adult round herring was examined, of which 39 were males and 32 were females. Based on this sample, the sex ratio did not differ significantly from 1:1 ($\chi^2 = 0.69$; $0.25<P<0.50$). Sixty-five specimens, from 93 to 165 mm SL, were collected in the Gulf of Mexico in August and November 1974. The 59 specimens more than 100 mm SL were maturing or near ripe. Six additional females, from 157 to 160 mm SL, that were collected in June 1973 off the east coast of Florida (lat. 30°20′N) were examined. Those six specimens were spent, the ovaries containing only small, clear, nucleated oocytes.

Ripening females usually have two modes of yolked oocytes (but occasionally only one), which apparently are both spawned during a single spawning season. Planktonic eggs were collected only from November through May. The spawning season extends from approximately 15 October to 31 May in the eastern Gulf of Mexico.

The fecundities of eight near-ripe females, 130-165 mm SL, were estimated, based on yolked oocytes present in ovaries (Table 3). Fecundities ranged from 7,446 to 19,699 and increased with size of the females. Relative fecundity (ova per gram body weight) ranged from 150 to 428 ova/g, the mean being 296.5 ova/g ($\bar{S}_x = 33.7$ ova/g). There was no apparent relationship between relative fecundity and either length or weight of females. The mean relative fecundity estimate, 296.5 ova/g, was used in subsequent adult biomass determinations. If all yolked oocytes were not

TABLE 3.—Fecundity estimates and related data from eight female round herring collected in the Gulf of Mexico, November 1974.

Specimen	Standard length (mm)	Weight (g)	Ovary weight (g)	Gonad index[1] (%)	Ovary sample weight (g)	Number ova in sample	Fecundity (ova)	Relative fecundity (ova/g)
1	165	55.60	1.13	2.03	0.030	523	19,699	354
2	138	34.82	0.36	1.03	0.025	709	10,210	293
3	152	44.41	0.41	0.92	0.025	454	7,446	168
4	149	40.65	1.10	2.71	0.035	553	17,380	428
5	161	55.20	0.60	1.09	0.020	276	8,280	150
6	143	37.97	0.43	1.13	0.025	781	13,433	354
7	130	29.62	0.65	2.19	0.035	535	9,936	335
8	144	37.28	0.33	0.89	0.025	818	10.798	290

[1]Gonad index is the ratio of ovary weight to weight of the female, expressed as a percentage.

spawned in a spawning season, the estimate of relative fecundity is too high and biomass estimates are low. Because no modes of yolked oocytes remained in ovaries of spent females from the June collection, I believe that yolked oocytes were spawned and that biomass estimates were not biased by this possible source of error.

Ito (1968) estimated mean fecundity of Japanese round herring to be 9,212 ova. His estimates were based only on the most advanced mode of yolked oocytes, although two modes usually were present. Ito's estimates are lower than the estimated fecundities of Gulf of Mexico round herring. Also, the diameters of near-ripe ova that he reported averaged 1.4 mm which is greater than that for spawned eggs in the Gulf of Mexico which average only 1.29 mm in diameter (Houde and Fore 1973). Diameters of ovarian ova reported by Ito (1968) are not in accord with those reported for pelagic eggs of Japanese round herring by Uchida et al. (1958), who gave the diameter as 1.25 mm. The length at first maturity, which Ito observed to be approximately 170 mm SL in Japanese specimens, exceeded that of my specimens by about 70 mm.

Time Until Hatching

Duration of the egg stage from spawning until hatching was estimated indirectly from the occurrence of three distinct embryonic stages during cruise IS 7303, at stations where surface temperatures were 21°-22°C. Spawning by round herring takes place at night, and early embryonic stages were collected only between midnight and 0400 e.s.t. Two other distinct embryonic stages were collected during those hours, one of which was a full-term embryo that was about to hatch. I assumed 2200 e.s.t. to be the peak spawning time. The time from spawning to hatching is approximately 2.1 days at 21°-22°C. Watson and Leis (1974) reported that Hawaiian round herring eggs incubated approximately 2 days when surface temperatures were in the range 23°-25°C.

The value of 2.0 days was used for hatching time in subsequent abundance estimation procedures (Equations (4), (5), and (8)). It probably overestimates duration for cruises during fall and spring, but it is a good estimate for the winter season when most spawning occurs. Overestimating duration would result in an underestimate of daily spawning and an underestimate of adult biomass. Because there were no data on duration of the egg stage for fall and spring cruises, I chose to accept a possible small bias of underestimating round herring biomass. O'Toole and King (1974) incubated South African round herring eggs at 11°-20.5°C. The eggs had been collected in plankton tows when surface temperature was 16.5°C. They estimated that round herring eggs hatched in 135 h at 11°C and 36 h at 20.5°C. They assumed that the blastodermal cap stage eggs, with which they began experiments, were only 4-6 h old. Gulf of Mexico round herring probably do not spawn at the low temperatures that O'Toole and King observed in South African waters. Temperatures as low as 16.5°C during the spawning season in the Gulf of Mexico occurred only at depths of 150 m and greater, on the outer edge of the continental shelf. Also, the rate of development of Gulf of Mexico eggs at temperatures above 20°C apparently is slower than that of South African eggs.

Cruise Egg Abundances

The estimated abundances of round herring eggs present in areas represented by each cruise are given in Table 4. Egg abundances, including all developmental stages, ranged from 0.24 to 209.31×10^{10} for cruises during the spawning season. No round herring eggs (or larvae) were collected on cruise CL 7405. That cruise was made

TABLE 4.—Abundance estimates of round herring eggs for each cruise. Estimates were obtained using Equations (2) and (3), and are not corrected for duration of the egg stage.

Cruise	Area represented by the cruise ($m^2 \times 10^9$)	Positive area[1] ($m^2 \cdot 10^9$)	Cruise egg abundance (eggs $\times 10^{10}$)
GE 7101	25.79	13.69	6.08
8C 7113			
TI 7114	120.48	21.80	0.24
GE 7117	101.10	0.00	0.00
8C 7120			
TI 7121	189.43	0.00	0.00
GE 7127			
8B 7132			
TI 7131	72.99	21.58	25.26
8B 7201			
GE 7202	148.85	78.43	209.31
GE 7208	124.88	15.79	1.51
GE 7210	48.43	0.00	0.00
IS 7205	104.59	0.00	0.00
IS 7209	149.80	17.79	1.37
IS 7303	149.80	78.19	38.49
IS 7308	151.42	10.52	4.04
IS 7311	156.50	0.00	0.00
IS 7313	153.18	0.00	0.00
IS 7320	153.89	31.34	6.33
CL 7405[2]	52.00	0.00	0.00
CL 7412	91.33	2.91	0.62

[1]Positive area is defined as the area representing stations where either eggs or larvae of round herring were collected.
[2]No stations on this cruise were located far enough offshore for round herring egg or larvae to have been collected.

during the spawning season, but because only nearshore stations were sampled, the round herring spawning area was not included in the cruise area. Abundance estimates in Table 4 are based on Equations (2) and (3). Cruise abundance estimates for eggs were used to estimate adult biomass in following sections.

Adjusting Cruise Egg Abundance Estimates

The cruise egg abundance estimates were adjusted for cruises GE 7127-TI 7131-8B 7132 and GE 7208. On these two cruises only a part of the round herring spawning area was sampled (Figures 3, 4). For cruise GE 7127-TI 7131-8B 7132 only 0.655 of the potential round herring spawning area was included, and for GE 7208 only 0.839 of the area was included. Abundance estimates for each of those cruises were adjusted by dividing the cruise egg abundance estimates (Table 4) by their respective area factors (0.655 or 0.839). Adjusted cruise egg abundance estimates are: (GE 7127-TI 7131-8B 7132)—38.56×10^{10}; (GE 7208)—1.80×10^{10}. The effect of adjusting egg abundance for these cruises had a minor effect on biomass estimation. Biomasses based on the adjusted and unadjusted egg abundance estimates were calculated and are compared in subsequent sections.

Annual Spawning and Biomass Estimates

Method I

The cruise abundance estimates (Table 4) were adjusted for duration of the egg stage by dividing each estimate by 2.0 days, the estimated time from spawning until hatching, to give estimates of daily spawning during each cruise (Table 5). Daily spawning estimates for each cruise were then expanded by Sette and Ahlstrom's (1948) method to a representative number of days (D_i defined in Equation (4)) in the spawning season of 15 October to 31 May (Table 5). Variance estimates on cruise and annual egg abundance were then obtained (Equations (4) and (6)). Finally, the estimated adult biomass was calculated (Equation (7)) (Table 5).

Estimates of biomass were obtained for 1971-72 and 1972-73 when sampling was carried out over the entire spawning seasons. Estimated biomass was 717,815 metric tons in 1971-72 but only 131,136 metric tons in 1972-73 (Table 5). The variance estimates are relatively low, but because only three cruises were made within the round herring spawning season and no estimates of day to day variation in spawning are available, there is a large source of unaccounted variation. The

TABLE 5.—Annual spawning and biomass estimates for round herring from the eastern Gulf of Mexico during the 1971-72 and 1972-73 spawning seasons. Estimates are based on the Sette and Ahlstrom's (1948) technique.

Spawning season	Cruise	Daily spawning estimate (eggs $\times 10^{11}$)	Days represented by cruise	Eggs spawned during cruise period ($\times 10^{11}$)	Variance estimates on spawned eggs ($\times 10^{24}$)	Adult biomass (metric tons)
1971-72	GE 7127					
	TI 7131					
	8B 7132	1.928	71.0	136.888	10.245	
	8B 7201					
	GE 7202	10.466	88.0	921.008	206.576	
	GE 7208	0.090	70.0	6.300	3.717	
Annual total			229	1,064.196	220.538	717,815
1972-73	IS 7209	0.069	64.5	4.451	1.787	
	IS 7303	1.925	91.0	175.175	34.470	
	IS 7308	0.202	73.5	14.847	4.100	
Annual total			229	194.473	40.357	131,136

number of days representing each cruise is large and spawning almost certainly was not uniform within each cruise period. This may account for the more than fivefold difference in biomass estimated during the 2 yr. On the other hand it is possible that biomass did differ greatly between the 2 yr. This is especially possible because the eastern Gulf may be an open-ended system with regard to round herring habitat. Round herring eggs and larvae were abundant in the north-central Gulf (Fore 1971) indicating that a large adult population is present there. If a single population of round herring inhabits the Gulf, the part found in the eastern Gulf might vary from year to year.

The area adjustments that had been made for two 1971-72 cruises, to account for part of the spawning area not being sampled, affected the biomass estimate in that spawning season. Without adjustments the biomass estimate was 685,273 metric tons rather than 717,815 metric tons. The effect of adjustment was to raise the estimate by more than 32,500 metric tons. This is only a 4.7% increase in estimated biomass.

It is unlikely that round herring biomass is as great as 1 million metric tons in the eastern Gulf of Mexico, but it probably is considerably in excess of 100,000 metric tons. Confidence limits, at the 0.95 probability level, based on the annual spawning variance estimates (Table 5) placed the probable range of round herring biomass between 517,470 and 918,160 metric tons in 1971-72 and between 45,430 and 216,840 metric tons in 1972-73.

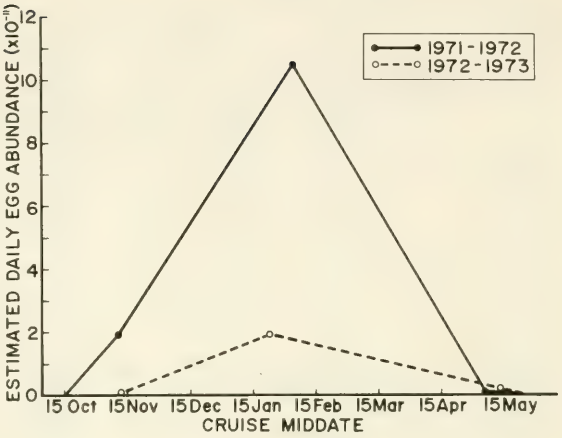

FIGURE 8.—Round herring egg abundance estimates in the eastern Gulf of Mexico based on three cruises in 1971-72 and 1972-73. Each symbol represents the estimated daily spawning at the middate of a cruise. The area enclosed by the polygons is an estimate of the total spawning by round herring during each of the seasons.

TABLE 6.—Annual spawning and biomass estimates for round herring from the eastern Gulf of Mexico during 1971-72 and 1972-73 spawning seasons. Estimates are based on the method described by Simpson (1959).

Spawning season	Cruise	Daily spawning estimate (eggs × 10^{11})	Annual spawning estimate (eggs × 10^{11})	Adult biomass (metric tons)
1971-72	GE 7127			
	TI 7131			
	8B 7132	1.928		
	8B 7201			
	GE 7202	10.466		
	GE 7208	0.090	1,034.852	698,045
1972-73	IS 7209	0.069		
	IS 7303	1.925		
	IS 7308	0.202	194.200	130,995

Method II

The daily spawning estimates for each of the three cruises during 1971-72 and 1972-73 were plotted against their cruise middates (Figure 8). Areas under the resulting polygons were determined and were equated to annual spawning (Table 6). This method is like that outlined by Simpson (1959). Biomasses were calculated using Equation (7).

Biomass estimates were 698,045 metric tons in 1971-72 and 130,995 metric tons in 1972-73 (Table 6). These estimates are similar to those obtained by Method I.

Method III

If spawning follows a normal distribution during the period 15 October to 31 May, then each cruise within that 229-day period can be represented as some proportion of the area under a normal curve with standard deviation of 38.17 days. Saville (1956, 1964) discussed use of the technique for a single cruise near the peak of the spawning season, but I have applied it (Equation (8)) to eight representative cruises during four round herring spawning seasons (Table 7). The observed variation within a season on annual spawning and biomass estimates is great. Although spawning is heaviest near the middle of the spawning season (Figure 8), it probably does not follow the normal distribution closely. It seems that in most years spawning intensity increases rapidly to near peak level during late November and then gradually decreases during spring months. Deviations from normality would cause large estimating errors, especially for cruises that

TABLE 7.—Annual spawning and biomass estimates for round herring from the eastern Gulf of Mexico during 1970-71 through 1973-74 spawning seasons. Estimates are based on the method of partitioning the spawning season into component parts of the normal curve (Saville 1956). The spawning season is assumed to be 229 days in length, ranging from 15 October to 31 May.

Spawning season	Cruise	Proportion of area under normal curve	Daily spawning estimate (eggs $\times 10^{11}$)	Days included in cruise	Annual spawning estimate (eggs $\times 10^{11}$)	Adult biomass estimate (metric tons)
1970-71	8C 7113					
	TI 7114	0.0057	0.012	12	25.270	17,046
1971-72	GE 7127					
	TI 7131					
	8B 7132	0.0081	1.928	11	2,618.258	1,766,110
	8B 7201					
	GE 7202	0.1153	10.466	11	998.436	673,481
	GE 7208	0.0072	0.090	10	125.310	84,526
Mean					1,247.335	841,373
1972-73	IS 7209	0.0072	0.069	9	85.592	57,735
	IS 7303	0.0857	1.925	9	202.109	136,330
	IS 7308	0.0041	0.202	9	443.798	299,358
Mean					243.833	164,474
1973-74	IS 7320	0.0067	0.316	9	425.198	286,811

were not made near the middle of the spawning season.

Mean biomass estimates for the 1971-72 and 1972-73 seasons were 841,373 and 164,474 metric tons, respectively (Table 7). These estimates do not differ much from those obtained by Methods I and II (Tables 5, 6). Also, it is interesting to note that the midwinter estimates in the 1971-72 (673,481 metric tons) and 1972-73 (136,330 metric tons) seasons, each based on a single cruise, gave estimates of round herring biomass nearly identical to those obtained by Methods I and II. A single cruise in January or February, with a subsequent biomass estimate by Method III, seems to be as good for obtaining estimates of round herring biomass as three cruises spaced over the entire spawning season. Multiple cruises within the November through February peak spawning period would, of course, be the best approach to gain precision in estimating biomass of this species from spawning surveys.

The annual spawning estimates, based on Method III from the eight cruises (Table 7), are log-normally distributed and an estimate of the mean biomass present from 1970 to 1974, with confidence limits at the 0.95-probability level, was calculated based on the eight $\log_{10}$ egg abundance estimates. Geometric mean annual spawning estimate for 1970-74 was $2{,}685.11 \times 10^{10}$ and the confidence limits are: $P(792.08 \times 10^{10} \leq P_a \leq 9{,}103.32 \times 10^{10}) = 0.95$. Expressed in terms of biomass, the geometric mean was 181,120 metric tons with confidence limits, $P(53{,}429 \leq B \leq 614{,}052) = 0.95$. If the arithmetic mean of the eight biomass estimates is considered a valid estimate of mean biomass, its value is 415,175 metric tons. A reasonable conclusion is that round herring biomass in the eastern Gulf is less than 1 million metric tons but probably greater than 100,000 metric tons.

Concentration of Biomass

The largest positive areas (i.e., areas where either round herring eggs or larvae were collected) occurred in cruises 8B 7201-GE 7202 and IS 7303 when more than 78×10^9 m^2 were in that category. This is nearly equivalent to the 76.5×10^9 m^2 in the survey area between 30- and 200-m depths that was determined by planimeter. The biomass of adult round herring is primarily located in the 30- to 200-m depth zone. If the confidence limits on biomass, based on Method I, are considered then biomass per unit area of sea surface must have been between 67.6 and 120.0 kg/hectare in 1971-72 and between 5.9 and 28.3 kg/hectare in 1972-73.

Potential Yield to a Fishery

Using Equation (9), the potential yield to a fishery, C_{max}, can be estimated, based on the range of biomass estimates that is available. Although the natural mortality coefficient, M, is not known, it probably lies between 0.50 and 1.00 for round herring in the eastern Gulf of Mexico. The estimated values of C_{max} if M equals 0.50, 0.75, or 1.00 are given in Table 8.

Potential yield estimates range from 32,749 to 420,687 metric tons (Table 8). The best estimates almost certainly lie midway between the extremes, so that 50,000-250,000 metric tons are in

TABLE 8.—Range of potential yield estimates for eastern Gulf of Mexico round herring, based on biomass estimates by three methods. Yields are predicted at three possible values of M, the natural mortality coefficient. Biomass estimates were obtained from values in Tables 5-7.

	Biomass estimating method and spawning season	Biomass estimate (metric tons)	Estimated potential annual yields (metric tons) for given values of M		
			$M = 0.5$	$M = 0.75$	$M = 1.0$
I	1971-72	717,815	179,454	269,181	358,908
I	1972-73	131,136	32,784	49,176	65,568
I	Mean of 1971-72 and 1972-73	424,476	106,119	159,179	212,238
II	1971-72	698,045	174,511	261,767	349,022
II	1972-73	130,995	32,749	49,123	65,498
II	Mean of 1971-72 and 1972-73	414,520	103,630	155,445	207,260
III	1971-72 mean	841,373	210,343	315,515	420,687
III	1972-73 mean	164,474	41,118	61,678	82,237
III	1971-72 cruises 8B 7201 and GE 7202	673,481	168,370	252,555	336,740
III	1972-73 cruise IS 7303	136,330	34,082	51,124	68,165
III	1970-74 geometric mean of 8 estimates	181,120	45,280	67,920	90,560
III	1970-74 arithmetic mean of 8 estimates	415,175	103,794	155,691	207,588

the range that I believe represents the mean potential annual yield of the stock. This is equivalent to a potential harvestable yield of 6.5-32.7 kg/hectare in the 76.5×10^9 m^2 of round herring habitat in the eastern Gulf. If stock size fluctuates greatly from year to year then the harvestable yield also may vary. As Alverson (1971) has pointed out, the biological potential yield is not necessarily the realizable yield. The realizable yield will depend upon the availability of the stock and its vulnerability to fishing gear. Neither of these factors has been evaluated for eastern Gulf round herring. It is possible that large year to year fluctuations in round herring biomass do occur, as suggested by the great differences in 1971-72 and 1972-73 biomass estimates. Such variation could reflect year class fluctuations or yearly changes in distribution of parts of the stock between the north-central and eastern Gulf. Although they are abundant, there is no reason to believe that round herring in the eastern Gulf constitute a stock as large as the Gulf menhaden stock in the north-central Gulf of Mexico, which produces a mean annual yield of more than 550,000 metric tons.

Larval Abundance Estimates

Larvae occurrence and abundance varied seasonally in the same manner as eggs (Table 9). The range of larvae abundances for positive cruises, including larvae in all length classes, was 0.47-31.95 $\times 10^{10}$. In subsequent estimates of larval

TABLE 9.—Abundance estimates of round herring larvae for each cruise. Estimates include larvae in all size classes and were obtained using Equations (2) and (3).

Cruise	Area represented by the cruise ($m^2 \times 10^9$)	Positive area[1] ($m^2 \times 10^9$)	Cruise larvae abundance (larvae $\times 10^{10}$)
GE 7101	25.79	13.69	2.58
8C 7113			
TI 7114	120.48	21.80	3.60
GE 7117	101.10	0.00	0.00
8C 7120			
TI 7121	189.43	0.00	0.00
GE 7127			
TI 7131			
8B 7132	72.99	21.58	2.92
8B 7201			
GE 7202	148.85	78.43	26.55
GE 7208	124.88	15.79	0.47
GE 7210	48.43	0.00	0.00
IS 7205	104.59	0.00	0.00
IS 7209	149.80	17.79	2.70
IS 7303	149.80	78.19	31.95
IS 7308	151.42	10.52	3.99
IS 7311	156.50	0.00	0.00
IS 7313	153.18	0.00	0.00
IS 7320	153.89	31.34	1.71
CL 7405[2]	52.00	0.00	0.00
CL 7412	91.33	2.91	5.09

[1]Positive area is defined as the area representing stations where either eggs or larvae of round herring were collected.
[2]No stations on this cruise were located far enough offshore for round herring eggs or larvae to have been collected.

abundance by length classes and in mortality estimation procedures, larval abundance by each 1-mm length class was adjusted for cruises GE 7127-TI 7131-8B 7132 and GE 7208 to account for only part of the potential round herring spawning area having been sampled. The adjustment factors were 0.655 and 0.839, the same factors that were used to adjust egg abundance for those cruises.

Larvae that were collected ranged from 2.1 to 30.0 mm SL during the survey. Length frequencies of larvae in the 2.1-20.0 mm SL range are illustrated in Figure 9. Larvae >20.0 mm were rarely collected during the survey. Frequencies for each length class in Figure 9 are given as estimated abundance during each cruise (Equation (3)). No area adjustments have been made in Figure 9 for the two cruises that did not cover the entire spawning area. Round herring larvae <4.0 mm SL usually were in poor condition, with curved or deformed bodies, and their measurements are underestimates of true length. O'Toole and King (1974) hatched eggs that they had collected and reported that preserved, newly hatched round herring larvae were 3.75-4.00 mm long. The 4.1- to 5.0-mm SL length class was the most abundant class in my survey (Figure 9). I assumed that this length class was fully vulnerable to the sampling gear, although some escapement may have occurred for larvae of this size.

The ratios of night-caught to day-caught larvae

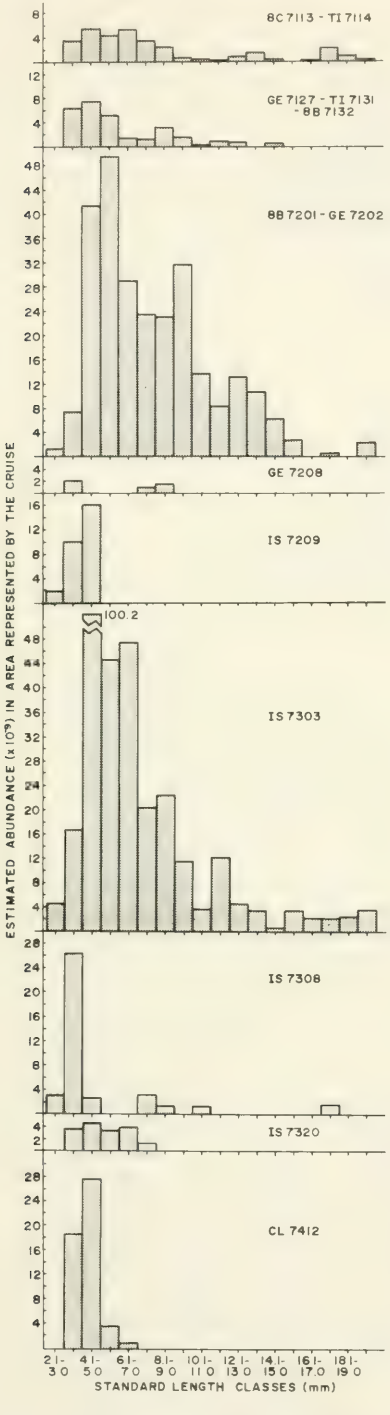

FIGURE 9.—Length-frequency distributions of round herring larvae for 1971-74 cruises to the eastern Gulf of Mexico. Frequencies are expressed as estimated abundance of larvae in each length class within the area represented by the cruise.

by length classes were examined over all cruises and they indicated that considerable net avoidance was occurring in the day relative to that occurring at night. The data were plotted by 2-mm length classes (Figure 10), and functions were fitted to allow estimation of the night-caught to day-caught ratio for larvae in any length class. The ratio increased rapidly for larvae of 4.0-13.0 mm, but then decreased from a factor of more than 3.0 to about 1.0 when larvae had grown to 18.0 mm. Two power functions were fitted: for larvae 2.1-14.0 mm SL the function was $R = 0.3041\ X^{0.9115}$, where R is the ratio of night-caught to day-caught larvae and X is standard length of larvae; for 12.1- to 20.0-mm SL larvae the function was $R = 44{,}521.54\ X^{-3.7298}$. Larva catches made at daytime stations were adjusted by R (Equation (11)). Exponential functions or a single polynomial could have been used in place of the power functions to describe the relationship, but the power functions provided reasonably good fits to the data and were acceptable for correction purposes. No adjustments were made for larvae <4.0 mm or >18.0 mm because there was no observable difference in night or day catches for larvae of those lengths.

The round herring larvae night to day catch ratios are unusual with respect to the observed

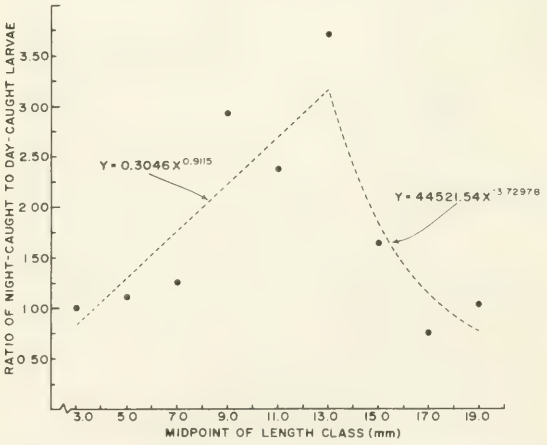

FIGURE 10.—Night to day ratios of sums of catches, standardized to numbers under 10 m² of sea surface, for round herring larvae collected in 1971-73 in the eastern Gulf of Mexico. The ratios were calculated for larvae within each 2-mm length class from 2.1 to 20.0 mm SL. Fitted power functions describe the relationships for larvae from 2.1 to 13.0 mm SL and for larvae from 13.1 to 20.0 mm SL. Larval abundance estimates for each length class at stations occupied during daylight were corrected by the appropriate ratio factor for each length class to account for daytime avoidance.

decrease in the ratio for larvae >13.0 mm. The ratio increased in other studies on clupeoid larvae throughout the size range of larvae that were collected (Ahlstrom 1954, 1959b; Lenarz 1973; Matsuura in press), and this is true for other species of clupeid larvae that I have studied in the Gulf of Mexico. The return of the ratio toward unity after round herring larvae reached 13.0 mm must indicate that larvae 13.0-18.0 mm became as good at avoiding the gear at night as during the day. The alternative explanation, which seems unlikely, is that larger larvae lost the potential to avoid the gear during daylight. Daylight is only one factor that could allow larvae to avoid the gear and adjustment of catches to account for it can only partially correct for avoidance losses. The correction was made, however, in an attempt to get the best estimate possible for round herring larval mortality during the 1971-72 and 1972-73 seasons.

Larval abundance estimates, corrected for daytime avoidance, were determined by 1-mm length classes for the 1971-72 and 1972-73 seasons (Figure 11) (Equation (10)). Except for larvae in the 4.1- to 5.0-mm length class, which were twice as abundant in 1972-73, total abundance of larvae was similar in the two seasons. The greater abundance of 4.1- to 5.0-mm larvae in 1972-73 could have reflected the reduction in towing speed from the previous season. Escapement of small larvae through the meshes may have been more important in 1971-72 when towing speed averaged about 0.7 knot faster.

Abundance of round herring larvae decreased exponentially as lengths increased during each season (Figure 11). Fitted exponential functions for 5.1- to 16.0-mm larvae in 1971-72 and 4.1- to 16.0-mm larvae in 1972-73 provided estimates of the instantaneous mortality coefficients per millimeter increase in length (Figure 11). The coefficients were $Z = 0.2269$ in 1971-72 and $Z = 0.3647$ in 1972-73. These correspond to percentage losses per millimeter increase in length of 20.3% in 1971-72 and 30.5% in 1972-73. Confidence intervals at the 0.95 probability level were $Z = 0.2269 \pm 0.0930$ in 1971-72 and $Z = 0.3647 \pm 0.1179$ in 1972-73. The null hypothesis of no difference in mortality coefficients between years was accepted at the $\alpha = 0.05$ probability level (t-test; $0.05<P<0.10$), but the t value was close to the rejection region suggesting that mortality may have been higher in 1972-73 than in 1971-72.

The mortality coefficients that I obtained are

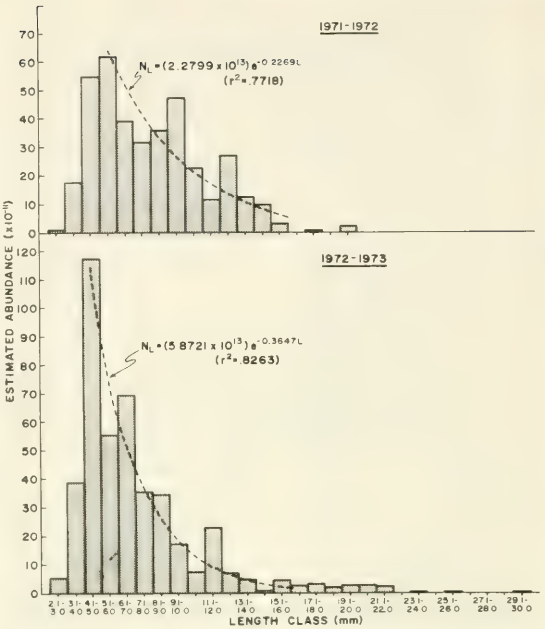

FIGURE 11.—Length-frequency distributions of annual larval abundance estimates of round herring larvae collected in the eastern Gulf of Mexico. Frequencies in each 1-mm length class are expressed as estimated annual abundance and have been corrected for daytime avoidance. Fitted exponential functions provide estimates of the instantaneous coefficient of decline in abundance by length, 1971-72 and 1972-73.

similar to those reported by Lenarz (1973) from several years of data on Pacific sardine and northern anchovy, *Engraulis mordax*. He reported a range of instantaneous coefficients of 0.15-0.33, averaging 0.22 for Pacific sardine, that correspond to a 20% loss per millimeter of growth. For anchovy his instantaneous coefficients ranged from 0.32 to 0.46, averaging 0.39, a mean decrease of 32% per millimeter of growth. Matsuura (in press) has measured the rate of decline in catches of Brazilian sardine, *Sardinella brasiliensis*, obtaining an instantaneous coefficient of 0.4962, corresponding to a 39% decrease in catch per millimeter of growth. Most of the decline in catch of larger round herring larvae presumably was due to larval mortality but gear avoidance also must be important. For this reason mortality curves were fitted only for larvae 16.0 mm or less in length. Catches of larger larvae were sporadic and possibly greatly influenced by gear avoidance.

Larval mortality is best expressed as a function of age. If it is assumed that growth of round herring larvae is exponential from the post yolk-sac

stage to 20.0 mm SL, then the instantaneous mortality coefficients, based on mean estimated ages of larvae, can be calculated using Equations (12)-(16). No information on growth rates of round herring larvae was available, but mean daily growth increments of other Gulf of Mexico clupeid species have been determined in laboratory rearing experiments and they range from 0.3 to 1.0 mm (Richards and Palko 1969; Saksena et al. 1972; Houde 1973b; Houde and Swanson 1975). Growth rates in those experiments exceeded 0.7 mm/day only when temperature was above 26°C. Mean daily growth of round herring larvae probably is between 0.3 and 0.7 mm. Duration of the egg stage from spawning until hatching is about 2.0 days. The duration of nonfully vulnerable length classes was estimated from a knowledge of growth rate and development times of other clupeid species that have been reared in the laboratory. Larvae of yellowfin menhaden, *Brevoortia smithi,* did not begin to grow in length until nearly 4 days after hatching at 26°C (Houde and Swanson 1975) when they were about 4.5 mm SL; larvae of *Harengula jaguana* did not grow significantly until they were nearly 3 days old and 4.5 mm SL at 26°-28°C (Houde et al. 1974). The exponential growth phase was assumed to begin in the 4.1- to 5.0-mm length class for round herring. The nonfully vulnerable length classes of 2.1-5.0 mm in 1971-72 were assigned durations that varied from 4.0 to 7.0 days; the nonfully vulnerable 2.1- to 4.0-mm length classes in 1972-73 were assigned durations of 1.5-3.0 days. Various combinations of mean daily growth increments and durations of nonfully vulnerable length classes were entered into the program to estimate mortality in relation to age of larvae (Equations (12)-(16)) for 1971-72 and 1972-73. Examples, for one combination of values of the variables in 1971-72 and one combination in 1972-73, are provided in Table 10 and Figure 12.

Given mean daily growth increments of 0.3-0.7 mm (corresponding to instantaneous growth coefficients of 0.0299-0.0698) and the most probable durations of nonfully vulnerable length classes, the probable range of instantaneous mortality coefficients was 0.0866-0.1739 in 1971-72 and 0.0835-0.1719 in 1972-73 (Table 11). In terms of daily mortality the 1971-72 probable estimates ranged from 8.3 to 16.0%; in 1972-73 they ranged from 8.0 to 15.8%. Although the estimated range is great, it is nearly the same for the two seasons. Varying duration of the nonfully vulnerable length classes had only minor effects on mortality rate estimation (Table 11), but varying the growth rate had important effects.

The values of N_0, the y-axis intercepts, provide yet another series of estimates of annual spawning, because they estimate the numbers of eggs present at time zero. The intercept values are generally lower than spawning estimates by the other methods and are not considered to be good estimates of spawning. It seems that the exponential model of loss fits the decrease in larval abundances reasonable well, but that a greater than expected mortality occurs between egg and fully vulnerable larval length classes. Figure 12 illustrates this possibility. If only larval mortality had been considered, rather than total mortality from egg to 16.0-mm larvae, the instantaneous coefficients

TABLE 10.—Two examples of data treated to obtain class durations and mean ages of round herring larvae from the eastern Gulf of Mexico. Abundance estimates are then corrected for duration, and the duration-corrected abundances were subsequently regressed on mean ages to obtain mortality rates (Table 11). Data are from 1971-72 and 1972-73 egg and larvae abundance estimates that were previously corrected for daytime avoidance. In these examples the mean daily growth increment ($\bar{b}$) was set at 0.50. The nonfully vulnerable length classes were 2.1-5.0 mm in 1971-72 with duration of 6 days, and 2.1-4.0 mm in 1972-73 with duration of 2.5 days. Calculating procedures are given in Equations (12)-(16). The regressions for these data are given in Figure 12.

1971-72					1972-73				
Class	Abundance (no. × 10^{11})	Duration (days)	Mean age (days)	Duration-corrected abundance (no. × 10^{11})	Class	Abundance (no. × 10^{11})	Duration (days)	Mean age (days)	Duration-corrected abundance (no. × 10^{11})
Eggs	2,128.39	2.00	1.00	1,064.20	Eggs	388.94	2.00	1.00	194.47
2.1-5.0	72.90	6.00	5.00	12.15	2.1-4.0	43.89	2.50	3.25	17.56
5.1-6.0	61.96	3.26	9.52	19.00	4.1-5.0	117.78	3.98	6.37	29.58
6.1-7.0	38.96	2.76	12.87	14.11	5.1-6.0	55.29	3.26	10.39	16.95
7.1-8.0	31.70	2.39	15.74	13.24	6.1-7.0	69.81	2.76	13.75	25.28
8.1-9.0	35.92	2.11	18.25	16.99	7.1-8.0	35.42	2.39	16.62	14.79
9.1-10.0	46.88	1.89	20.48	24.77	8.1-9.0	34.55	2.11	19.13	16.34
10.1-11.0	22.29	1.71	22.49	13.02	9.1-10.0	17.08	1.89	21.36	9.02
11.1-12.0	11.60	1.56	24.32	7.41	10.1-11.0	7.44	1.71	23.37	4.34
12.1-13.0	26.81	1.44	25.99	18.63	11.1-12.0	22.99	1.56	25.20	14.70
13.1-14.0	12.25	1.33	27.53	9.19	12.1-13.0	6.67	1.44	26.87	4.63
14.1-15.0	9.89	1.24	28.97	7.97	13.1-14.0	4.79	1.33	28.41	3.59
15.1-16.0	3.31	1.16	30.31	2.85	14.1-15.0	0.74	1.24	29.85	0.59
					15.1-16.0	4.36	1.16	31.19	3.76

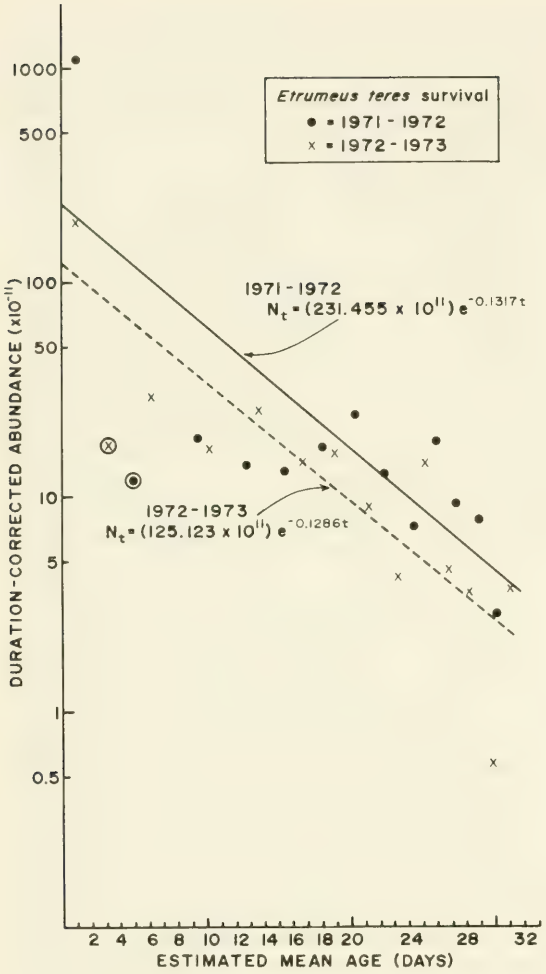

FIGURE 12.—Estimated abundance of egg and larval stages of round herring in the eastern Gulf of Mexico in 1971-72 and 1972-73. Abundance is expressed as a function of estimated age. Fitted exponential functions give estimates of the instantaneous rates of decline in abundance for eggs and larvae up to 31 days of age. The two symbols enclosed in circles represent nonfully vulnerable length classes and were not included in the regression estimates of instantaneous decline.

would have been lower. In 1971-72, $Z = 0.0563$ for fully vulnerable larval stages and $Z = 0.1123$ for those stages in 1972-73. The results suggest that egg and nonfully vulnerable larvae mortality were higher in 1971-72 than in 1972-73. Mortality of vulnerable larval stages appears to have been higher in 1972-73 when the population declined by 10.6%/day as opposed to 1971-72 when it declined only 5.5%/day. The higher mortality rate of larvae in 1972-73 also was apparent in the mortality estimates based on larval lengths (Figure 11).

High mortality of eggs or newly hatched larvae may be characteristic of many clupeids, including round herring. Smith (1973) recently reported that Pacific sardine eggs experience high mortality, the instantaneous rate being $Z = 0.31$ during that stage. Pilchard, *Sardina pilchardus*, eggs undergo high mortality during early embryonic stages (Southward and Demir 1974) and embryos of *Clupeonella delicatula* suffered high mortality, especially under unfavorable temperature regimes (Pinus 1974).

The best probable estimates of mortality from the egg to 16.0-mm larval size are near the middle of the ranges given in Table 11, at instantaneous growth rates of 0.0498. In 1971-72, $Z = 0.1317$ is the most probable estimate while $Z = 0.1286$ seems most probable in 1972-73. These estimates correspond to average daily losses of 12.3% in 1971-72 and 12.1% in 1972-73. Estimates of the instantaneous mortality coefficients based on the two examples given in Table 10 and Figure 12 coincide with what I believe may be the best estimates of mortality. Confidence limits, at the 0.95 probability level, were placed on the instantaneous mortality coefficients derived from these examples. They were wide, ranging from $Z = 0.0635$-0.1999 in 1971-72 and $Z = 0.0823$-0.1749 in 1972-73. The coefficients $Z = 0.1317$ in 1971-72 and $Z = 0.1286$ in 1972-73 did not differ significantly between years (t-test; $P > 0.50$).

The estimates of mortality rates could be too high if avoidance by larvae was increasing significantly as they grew, reducing their probability of capture. If growth was not exponential, but linear, during the larval phase, then the mortality estimates may be too low, because duration-corrected abundances gave relatively high values to older larvae that presumably were growing through length classes at an increasing rate.

Because of the difficulty in ageing eggs or larvae of marine fishes, few estimates of mortality rates in relation to age have been reported. Ahlstrom (1954) reported that about one Pacific sardine larva survived to 21.25 mm/100,000 eggs spawned during the first 40-45 days of life, which corresponds to an instantaneous daily loss rate of 0.16-0.17. Japanese sardine was investigated by Nakai and Hattori (1962). They reported survival from egg to the 15.0 mm stage as 0.10% in 54 days, corresponding to an instantaneous rate of $Z = 0.1279$. This rate is nearly identical to that which

TABLE 11.—Summary of mortality estimates for round herring larvae from the eastern Gulf of Mexico, 1971-72 and 1972-73. Estimates were obtained from the exponential regression of egg and larvae abundances on mean age. Instantaneous growth and mortality coefficients were calculated for various possible combinations of mean daily growth increment and duration of the nonfully vulnerable larval stages. Egg stage duration was assumed to be 2.0 days. Nonfully vulnerable larval stages were 2.1-5.0 mm SL in 1971-72 and 2.1-4.0 mm SL in 1972-73. Explanation of the estimating method is given in Equations (12)-(16).

Season	Mean daily growth increment (mm)	Instantaneous growth coefficient (g)	Nonfully vulnerable larvae duration (days)	Instantaneous mortality coefficient (Z)	Y-axis intercept, N_0 (no. $\times 10^{11}$)	Daily mortality rate, $1 - \exp(-Z)$
1971-72	0.3	0.0299	4.0	0.0866	103.25	0.0830
	0.3	0.0299	5.0	0.0866	112.07	0.0830
	0.3	0.0299	6.0	0.0866	121.40	0.0830
	0.3	0.0299	7.0	0.0866	131.21	0.0829
	0.5	0.0498	4.0	0.1331	186.35	0.1246
	0.5	0.0498	5.0	0.1325	208.29	0.1241
	0.5	0.0498	6.0	0.1317	231.46	0.1234
	0.5	0.0498	7.0	0.1307	255.74	0.1225
	0.7	0.0698	4.0	0.1739	285.65	0.1596
	0.7	0.0698	5.0	0.1718	324.45	0.1579
	0.7	0.0698	6.0	0.1693	364.72	0.1558
	0.7	0.0698	7.0	0.1665	406.00	0.1534
1972-73	0.3	0.0299	1.5	0.0842	71.56	0.0808
	0.3	0.0299	2.0	0.0840	73.89	0.0805
	0.3	0.0299	2.5	0.0837	76.26	0.0803
	0.3	0.0299	3.0	0.0835	78.68	0.0801
	0.5	0.0498	1.5	0.1303	114.55	0.1222
	0.5	0.0498	2.0	0.1295	119.80	0.1214
	0.5	0.0498	2.5	0.1286	125.12	0.1207
	0.5	0.0498	3.0	0.1278	130.52	0.1200
	0.7	0.0698	1.5	0.1719	160.03	0.1580
	0.7	0.0698	2.0	0.1702	168.78	0.1565
	0.7	0.0698	2.5	0.1683	177.58	0.1549
	0.7	0.0698	3.0	0.1665	186.39	0.1533

is most probable for round herring larvae. Harding and Talbot (1973) and Bannister et al. (1974) reviewed the results of several years' investigations on plaice, *Pleuronectes platessa*. They found that instantaneous mortality coefficients varied from only 0.0209 to 0.0685 from egg stage 1 to larval stage 4 during the long larval life of more than 150 days. Mortality of haddock eggs and larvae was reported by Saville (1956), who gave a series of estimates that ranged from 4 to 16%/day (Z = 0.04-0.17) during a 4-yr survey of egg and larvae abundance at Faroe. Jack mackerel, *Trachurus symmetricus*, larvae have a high rate of mortality (Lenarz 1973), losses ranging from 57 to 67% per millimeter of growth. Farris (1961) reported mortality of jack mackerel larvae in relation to age. The instantaneous mortality rate, calculated from his data, was 0.23 during the first 30 days of life. Mortality of Japanese mackerel, *Scomber japonicus*, larvae was very high (Watanabe 1970), 99.95% mortality having occurred between the egg and 15-mm larval stage in about 23 days. This corresponds to an instantaneous rate of $Z = 0.3295$. Round herring larval mortality rates apparently are similar to those of other clupeoids from temperate or subtropical marine waters (Ahlstrom 1954; Nakai and Hattori 1962; Lenarz 1973). On average they are slightly higher than those reported for haddock (Saville 1956). Round herring larvae have mortality rates that are much higher than those reported for North Sea plaice larvae and lower than those reported for jack mackerel or Japanese mackerel larvae.

If any period can be considered critical in the early life of round herring, it must occur between the time that eggs are spawned and when larvae reach 5.5 mm long. Greatest losses occurred at that time in 1971-72 and 1972-73 (Figure 12). Abundance estimates declined by more than 92% between the egg and 5.5-mm larvae in 1971-72. A decline of more than 78% in abundance was estimated between egg and 5.5-mm larvae in 1972-73 (Table 12, Figure 12). For larvae longer than 5.5 mm mortality decreased, the decrease in rate being especially great in 1971-72.

The number of survivors and percentage survival of round herring larvae at various stages were estimated (Table 12) from the number of spawned eggs obtained by Method I and the information on growth and mortality that is summarized in Table 11. The Method I spawning estimate was assumed to be a better estimate of initial number of eggs than the y-intercept estimates in Table 11. There was an apparent high mortality between spawning and hatching which exceeded 75% in 1971-72 (Table 12). The larval populations were reduced by

TABLE 12.—Estimated numbers and percentages of survivors of round herring larvae at hatching, 5.5 mm SL and 15.5 mm SL in 1971-72 and 1972-73. Estimates are made for three possible growth rates (see Table 11). Duration of the nonfully vulnerable larval stages was set at 6.0 days for 2.1-5.0 mm larvae in 1971-72 and 2.5 days for 2.1-4.0 mm larvae in 1972-73. The number of spawned eggs in each year was based on estimates by Method I (Table 5). Predicted numbers at hatching, 5.5 mm and 15.5 mm are calculated from exponential functions based on Table 11 data.

Season	Instantaneous growth coefficient (g)	Number of spawned eggs ($\times 10^{11}$)	Instantaneous mortality coefficient (Z)	Number hatching ($\times 10^{11}$)	% mortality to hatching[1]	Number of 5.5-mm larvae ($\times 10^{11}$)	% mortality to 5.5 mm	Number of 15.5-mm larvae ($\times 10^{11}$)	% mortality to 15.5 mm
1971-72	0.0299	1,064.20	0.0866	102.09	90.3	48.77	95.4	2.43	99.8
	0.0498	1,064.20	0.1317	177.86	83.3	66.06	93.8	4.27	99.6
	0.0698	1,064.20	0.1693	259.96	75.6	78.40	92.6	6.35	99.4
1972-73	0.0299	194.47	0.0837	64.51	66.8	23.00	88.2	1.26	99.3
	0.0498	194.47	0.1286	96.74	50.3	32.89	83.1	2.27	98.8
	0.1683	194.47	0.1683	126.83	34.8	41.00	78.9	3.37	98.3

[1]Hatching assumed to occur at 2.0 days.

more than 99.4% at 15.5 mm in 1971-72 and by more than 98.3% in 1972-73. The 15.5-mm stage would be attained at about 31 days if the instantaneous growth coefficient was 0.0498 (equal 0.5-mm mean daily growth increment). At that growth rate, approximately 4 larvae/1,000 eggs spawned in 1971-72 and 12 larvae/1,000 eggs spawned in 1972-73 would have survived to 15.5 mm and 1 mo of age.

SUMMARY

1) Surveys of eggs and larvae were used to investigate spawning, to determine adult stock size, and to study aspects of the early life history of round herring in the eastern Gulf of Mexico during 1971-74.

2) Spawning takes place from mid-October to the end of May between the 30- and 200-m depth contours. About 60% of the total spawning occurred at depths greater than 50 m. Most spawning apparently occurred during January and February.

3) Eggs occurred when surface temperatures ranged from 18.4° to 26.9°C, and surface salinities from 34.5 to 36.5‰. Larvae ≤5.0 mm SL were collected when surface temperatures were from 20.5° to 26.9°C, and surface salinities from 34.1 to 36.8‰. Of the eggs 82.5% and of the ≤5.0-mm larvae 87.5% were collected when surface temperatures were from 21° to 26°C. More than 50% of the eggs and ≤5.0-mm larvae were collected where surface salinity exceeded 36.0‰.

4) There is a major spawning area between lat. 27°00′ and 28°00′N and long. 083°30′ and 084°30′W. The center of the area is located about 150 km west by southwest of Tampa Bay in depths of 50-200 m.

5) The fecundity of eight round herring females 130-165 mm SL ranged from 7,446 to 19,699. Mean relative fecundity was 296.5 ova/g ($S_{\bar{x}}$ = 33.7). Gonads of round herring collected from August to November were ripening or near ripe. Those collected in June were spent. The sex ratio of 71 round herring adults did not differ significantly from 1:1.

6) The time from spawning to hatching, based on observations of development stages in planktonic eggs, was about 2.0 days at 22°C.

7) Adult biomass was determined by three methods from data on estimated annual spawning. The Sette and Ahlstrom's (1948) and Simpson's (1959) techniques gave estimates that ranged from 130,000 to 715,000 metric tons in 1971-72 and 1972-73. The geometric mean of eight individual estimates by Saville's (1956) method was 181,200 metric tons, the arithmetic mean being 415,175 metric tons. But, the best estimates by Saville's method were from two individual cruises in midwinter. These were 673,481 metric tons in 1971-72 and 136,330 metric tons in 1972-73. Those estimates were nearly the same as estimates obtained by the other two methods. Spawning biomass apparently was higher in 1971-72 than in 1972-73.

8) The estimated concentration of biomass between the 30- and 200-m depth contours, based on the stock size estimates, was from 67.6 to 120.0 kg/hectare in 1971-72 and from 5.9 to 28.3 kg/hectare in 1972-73.

9) The annual potential yield of round herring to a fishery, if instantaneous natural mortality coefficients lie in the range 0.5-1.0, ranged from 32,750 to 420,700 metric tons. The most probable mean annual potential yield estimates are in the range 50,000 to 250,000 metric tons. This is equivalent to 6.5-32.5 kg/hectare in the 30- to 200-m depth zone.

10) Total abundance of larvae was estimated in 1971-72 and 1972-73. The 4.1- to 5.0-mm length

class was nearly twice as abundant in 1972-73 as in 1971-72. Other length classes were somewhat more abundant in 1971-72 catches.

11) Mortality rates of larvae were estimated by length and for estimated ages. For lengths, the instantaneous coefficients of decline in catches were $Z = 0.2269$ in 1971-72 and $Z = 0.3647$ in 1972-73, corresponding to 20.3 and 30.5% losses per millimeter of growth. For ages, a range of estimates of daily mortality, based on varying growth rates and nonfully vulnerable larva stage durations, was obtained. The most probable daily mortality estimates were $Z = 0.1317$ in 1971-72 and $Z = 0.1286$ in 1972-73, corresponding to percentage losses of 12.3 and 12.1% on a daily basis.

12) It is probable that more than 99.4% mortality from eggs to 15.5-mm larvae occurred in 1971-72, and that more than 98.3% mortality occurred during that period in 1972-73. About 4 larvae/1,000 eggs spawned survived to 31 days and 15.5 mm in 1971-72, while about 12 larvae/1,000 eggs survived to that stage in 1972-73.

ACKNOWLEDGMENTS

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REPRODUCTIVE BIOLOGY OF THE FEMALE DEEP-SEA RED CRAB, *GERYON QUINQUEDENS*, FROM THE CHESAPEAKE BIGHT[1,2]

PAUL A. HAEFNER, JR.[3]

ABSTRACT

Collections of the deep-sea red crab, *Geryon quinquedens*, were made at depths from 270 to 1,300 m in the vicinity of Norfolk Canyon in the northwest Atlantic Ocean in November 1974, September 1975, and January 1976. The gross morphology and histology of ovary development are described. The size range in which relative growth of the abdomen changes is associated with maturation of the vulvae, copulation and insemination, gonad development, and egg extrusion. Females become sexually mature within the intermolt size range 65-75 mm carapace length (80-91 mm carapace width). Most intermolt females ≥76 mm carapace length show signs of copulation and insemination, and their ovaries are in intermediate to advanced stages of development. Few females <75 mm are ovigerous.

Historically the red crab, *Geryon quinquedens* Smith, has been seldom utilized commercially (Schroeder 1959; McRae 1961). Explorations have established that red crabs can readily be captured by pot or trap fishing in many regions along the eastern United States. The commercial potential of this crab has spurred investigations of the general biology and distribution (Le Loeuff et al. 1974; Haefner and Musick 1974; Wigley et al. 1975; Gray[4]; Dias and Machado[5]; Ganz and Herrmann[6]) as well as technological and economic aspects of harvesting and processing (Meade and Gray 1973; Holmsen and McAllister 1974).

The present study was prompted by recognition that biological data on sexual maturity are required for proper management of red crab stocks. This paper presents data on collections from Chesapeake Bight and deals with various aspects of reproductive biology of the female crab: ovary development, size composition of catch, size of ovigerous individuals, abdomen width-carapace length relationship, development of vulvae, and evidence of copulation and insemination.

METHODS

Red crabs were collected at depths from 270 to 1,300 m in Norfolk Canyon and vicinity (lat. 36°32′-37°10′N; long. 74°10′-74°46′W) in November 1974 (RV *James M. Gilliss* 74-04), September 1975 (RV *James M. Gilliss* 75-08), and January 1976 (RV *James M. Gilliss* 76-01). Based on the recommendations of Gray (see footnote 4), all female crabs were measured for short carapace length (CL, distance from the diastema between the rostral teeth to the posterior edge of the carapace, along the midline); width of the fifth abdominal segment was recorded for 190 crabs. Carapace length may be converted into carapace width (CW) by using the equation $CW = 11.04 + 1.06CL$, $r = 0.98$, based on measurements of 268 female crabs.

Pleopods and vulvae were examined to determine if mating and egg extrusion had occurred. Eggs or egg remnants or their absence on pleopods, variations in the size, shape and physical condition of vulvae, and the relative size of seminal receptacles were noted. Selected samples of the spermathecal fluid were withdrawn directly from incisions in the receptacle and examined microscopically for presence of sperm or spermatophores.

Ovaries were initially classified to relative size following the scheme used for the rock crab, *Cancer irroratus* (Haefner 1976). The scheme for

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[2]Contribution No. 777, Virginia Institute of Marine Science, Gloucester Point, VA 23062.

[3]Virginia Institute of Marine Science, Gloucester Point, VA 23062.

[4]Gray, G. W., Jr. 1969. Investigation of the basic life history of the red crab (*Geryon quinquedens*). R.I. Div. Conserv. P.L. 88-309, Proj. 3-46-R Completion Rep., 36 p.

[5]Dias, C. A., and J. S. Machado. 1974. Preliminary report on the distribution and relative abundance of deep-sea red crab (*Geryon* sp.) off Angola. Sci. Pap. No. 26, 12 p. *In* Scientific papers presented to the second session of the International Commission for the Southeast Atlantic Fisheries (Madrid, December 1973). Publ. Mimeogr. M. E. Bioceanol. Pescas, Angola 12, 75 p.

[6]Ganz, A. R., and J. F. Herrmann. 1975. Investigations into the southern New England red crab fishery. R.I. Dep. Nat. Resour. Div. Fish. Wildl. Mar. Fish. Sect., 78 p.

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red crabs was quantified by measuring ovary volume and deriving gonad indices (Giese and Pearse 1974) for the various stages. Certain ovarian samples were selected on the basis of relative size and color and treated in the following manner. Displacement of ovaries was measured by placing the entire, excised ovary in volumetrically graduated tubes containing a known quantity of seawater. Ovary volume (V_o in milliliters) was used to compute a gonad index: G_i = (Ovary weight)/(Total body weight) × 100, where weights in grams were calculated as follows Ovary weight = 1.025 V_o, assuming ovarian specific gravity equals that of seawater. Total body weight was derived from the following relationship based on measurements of 142 females: log body weight = −3.134 + 2.8833 log length, r = 0.968.

Portions of the ovaries were then preserved in Davidson's fixative for histological processing and in Gilson's fluid (Bagenal and Braum 1971) for measurement of ova size.

Histological sections were stained in haematoxylin and eosin and mounted in Permount.[7] Descriptions of developmental stages were made from the resultant slides.

Samples in Gilson's fluid were shaken to release ova which were then observed with a dissecting microscope. The diameters of 20 spherical ova from each sample were measured with a calibrated ocular micrometer. Misshapen ova were not considered. Similarly, 20 extruded eggs from 11 ovigerous crabs were removed and measured (length and width). A mean diameter was computed for each crab.

[7]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS AND DISCUSSION

The Ovary

The following account of the gross morphology and histology of the red crab ovary is based on examination of the gross anatomy of 255 crabs and on histological preparations from 34 crabs.

The ovary is an H-shaped organ located dorsally just beneath the carapace (Figure 1). Two horns extend anterolaterally from either side of the gastric mill and lie dorsal to the hepatopancreas. At the posterolateral borders of the gastric mill, near the origin of the posterior mandibular muscle bundles, the anterior horns are joined by a commissure. Two posterior horns, which lie ventral to the heart, extend posteriorly on either side of the intestine. The seminal receptacles arise from the midlateral border of the posterior horns and open externally through gonopores (vulvae) on thoracic sternite VI, immediately adjacent to sternite V.

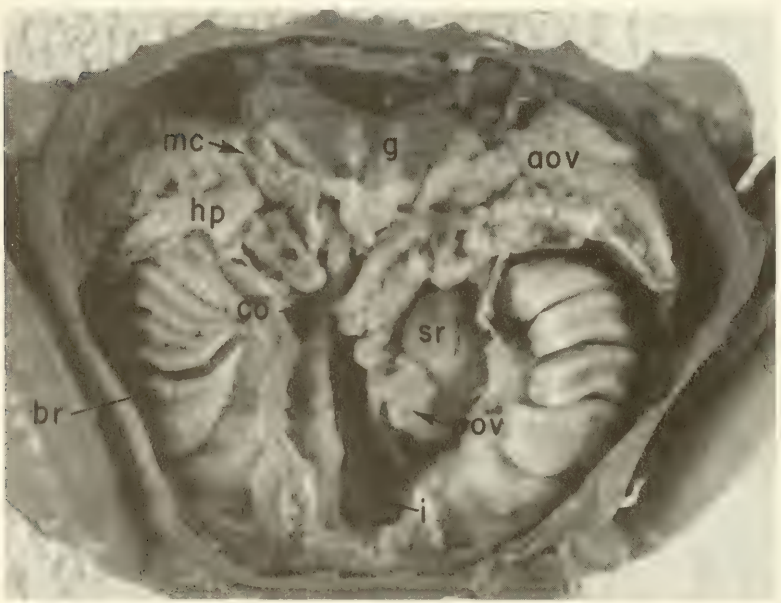


FIGURE 1.—Dorsal dissection of female *Geryon quinquedens*. Heart and medial portion of branchial chamber removed. Anterior (aov), posterior (pov) and commissure (cov) of ovary, gastric mill (g), gill (br), intestine (i), hepatopancreas (hp), seminal receptacle (sr), midgut caeca (mc).

Very Early Development

In very early development (Table 1), the ovary is small (<0.2 ml in volume; horn width 0.5 mm) and colorless. A central lumen is not apparent from gross morphological examination, although the precursor of one is indicated in Figure 2. Lobation is not obvious in this stage. The bulk of the organ consists of fibrous connective tissue, apparently stratified, and blood sinuses (Figure 2A). The outer connective tissue wall of the ovary is not readily distinguishable from the inner connective tissue. Various cell types are present. Most cells contain one oval nucleus (7.2 μm long) while other larger, less numerous cells have a large round nucleus (7.2 μm in diameter). Ova diameters are small (40-172 μm) and confined to germinative areas or strands. In some instances, it is difficult to free the ova from the surrounding tissue even after treatment in Gilson's fluid. The germinal zone consists of columnar cells with (12 μm) elongate nuclei (Figure 2B).

Early Development

White, ivory, light gray, or light yellow ovaries which are small (0.2-2.0 ml volume, 2-6 mm horn width) may exhibit histological development in advance of the previous stage. Most of the organ is filled with ova in various early stages of development (Figure 3A). Connective tissue is still prevalent around the margin, penetrating the ovary in numerous locations to form small lobes which are not readily visible from a gross morphological aspect.

The germinal zone is well defined and branches throughout the ovary. Cells in an early stage of oogenesis, recognizable by vacuolate nuclei (Figure 3B), are small (14-53 μm) compared with the more advanced ova (74-278 μm) characterized by more compact nuclei and the presence of cytoplasmic yolk granules (Figure 3C, D). They are surrounded by a single layer of follicular cells (Figure 3D) which are spindle shaped with an elongate nucleus (72 μm).

Intermediate Stage

As the ovary progresses to the intermediate stage of development, accumulating yolk, it gradually occupies more space (G_i = 1.4-2.7) in the visceral cavity and changes color (Table 1). The ovarian architecture is little changed from that of earlier stages; connective tissue is confined to the margin of the ovary and to the interstices between the now obvious lobes. Germinative zones are present. Ova are larger (112-537 μm) than those in earlier stages.

Mature Stages

A fully mature ovary nearly obscures the hepatopancreas in dorsal view. Only a small portion of the hepatopancreas and the slightly coiled midgut caecae are visible between the ovary and branchial chamber (Figure 1). The high gonad indices (>2.7) attest to the large volume (8-32 ml) of the organ at these stages of development. The color remains variable but is generally darker than that of earlier stages as reddish and brownish hues become evident (Table 1).

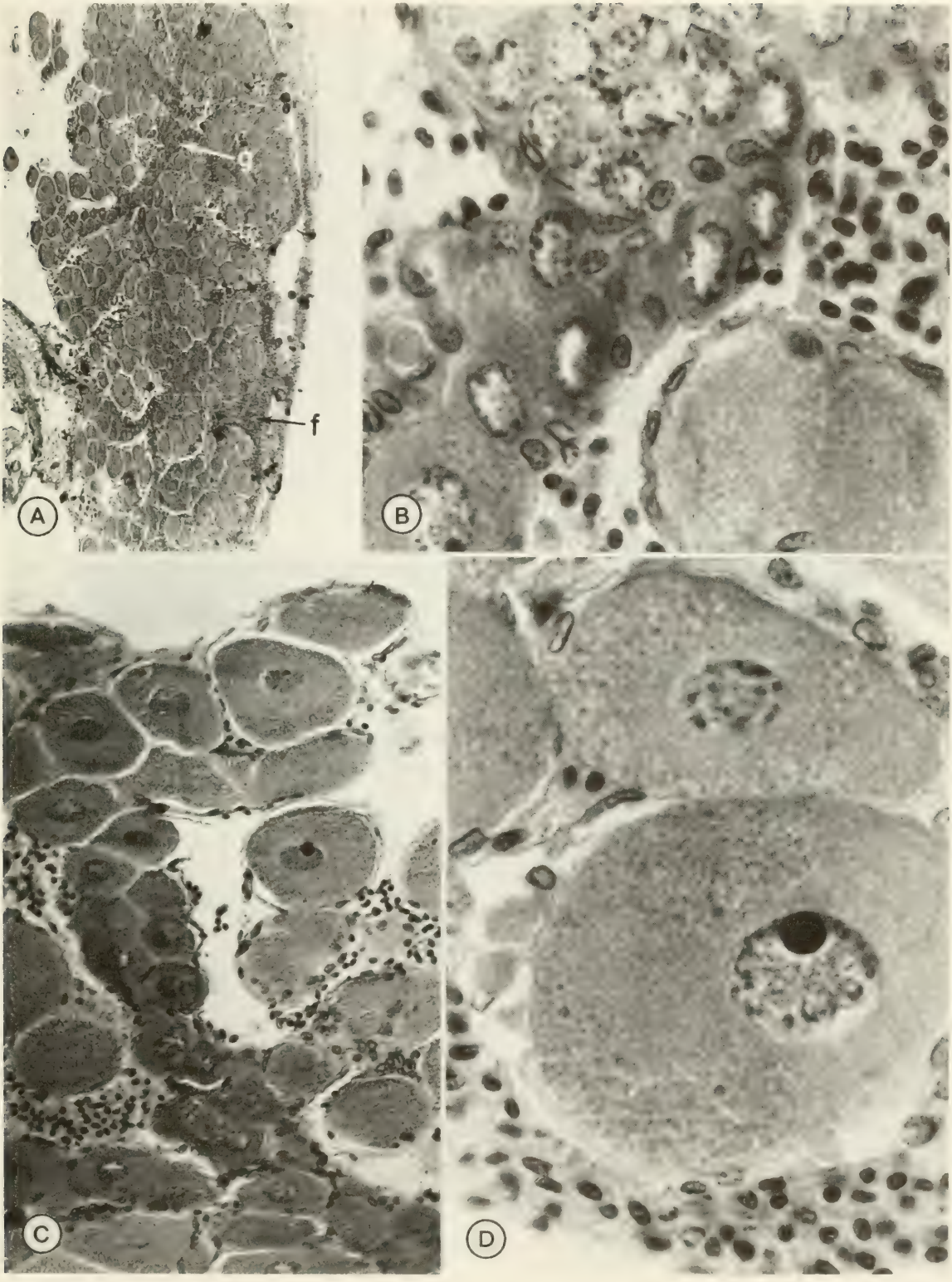
The predominant histological feature in a

TABLE 1.—Descriptive stages of *Geryon quinquedens* ovary: color variation, horn size, volume, gonad index, and ova diameter.

Stage of ovary development	Color of ovary	Horn width range (mm)			Ovary volume (ml)			Gonad index			Ova diameter (μm)		
		n	Ant.	Post.	*n*	$\bar{X}$	Range	*n*	$\bar{X}$	Range	*n*	$\bar{X}$	Range
Very early	Colorless, white, ivory	7	0.5-2.2	0.5-1.3	8	<0.2	0.1-0.2	8	0.29	0.09-0.88	3	102	49-172
Early	White, ivory, light gray, light yellow	12	2-6	2-6	15	1.1	0.2-2	15	0.75	0.19-1.75	10	168	74-278
Intermediate	Ivory, white, light yellow, yellow, yellowish orange, light brownish orange	7	8-15	6-10	12	5.2	4.5-7	12	2.05	1.45-2.73	10	289	112-537
Advanced	Yellow, yellowish orange, brownish orange, reddish brown, brownish purple	4	16-23	6-12	6	13.4	8-12	6	4.24	2.74-6.02	6	508	298-666
Mature	Yellowish orange, orange, brownish orange, brownish purple	12	20-32	10-18	10	28.9	21-32	11	8.22	6.00-11.85	9	611	484-788
Redeveloping	Ivory, yellowish orange, light brownish orange, reddish brown, reddish orange, brownish purple	6	8-20	5-7	14	9.0	2.5-21	14	2.67	1.04-7.25	16	347	148-671

FIGURE 2.—Ovary of *Geryon quinquedens* in very early development stage. A. 25×. Fibrous connective tissue (f) predominates. Germinal strand (g) and lumen (l) precursors are present. B. Enlargement (400×) of germinal strand region showing columnar cells.

FIGURE 3.—Ovary of *Geryon quinquedens* in early development stage. A. 25×. Ova in various stages of development are shown radiating from germinal zone (g). Fibrous connective tissue (f) evident. B. High magnification (400×) emphasizing vacuolar nucleate cells in early stages of oogenesis. C. Follicular development (125×) in early stage ovary. Yolk granules evident in larger ova. D. High magnification (400×) showing yolk granular consistency of cytoplasm in developing ova.


f
A
B
C
D

mature ovary, usually brownish orange to brownish purple, is the concentration of large ova (484-788 μm) containing large yolk granules which make sectioning difficult. The size range of these ova overlaps the mean diameter range of extruded eggs (638-817 μm).

The ovary is subdivided into lobes and possesses a central hollow shaft or lumen as described for *Callinectes sapidus* by Cronin (1942) and for *Portunus sanguinolentus* by Ryan (1967). An irregular matrix of compact germinal tissue, surrounded by less compact zones of large ova, borders the lumen.

Redeveloping Ovaries

The presence of developing ova in germinal zones of ovaries suggests that oogenesis continues after ovulation. Such redevelopment is indicated by the range of ovarian developmental stages observed in crabs known to have ovulated. Ovaries from seven ovigerous crabs with egg remnants resembled the early to advanced stages described above. Mean values and ranges of horn width, ovary volume, and gonad index reflect the wide variety of stages of redevelopment (Table 1).

In ovaries from nine ovigerous crabs and seven females with egg remnants on the pleopods, germinative zones were clearly evident (Figure 4A) but the ovary was less compact than that of the mature or ripe ovary as the interstices were filled with connective tissue (Figure 4B). The ova were more variable in size within a given developmental stage. Relatively large ova (388 μm) can be found in an early stage ovary while unusually small ova (168 μm) are numerous in an advanced ovary.

Incidence of Ovarian Development

A relationship exists between size of female and ovarian development (Figure 5). Eighty-eight percent of all crabs ≤75 mm CL (91 mm CW) possessed ovaries in early stages of development; 90% of the females >75 mm were in intermediate to advanced stages of ovarian development. Early developmental stages can occur in large crabs, particularly after recent ovulation. This is evident from the distribution of ovigerous crabs and those with egg remnants on the pleopods. Such ovaries, in redevelopment stages, can recede to early developmental stages.

Size at Sexual Maturity

Hartnoll (1969) regarded a crab as mature "when it enters the intermolt during which it is first able to copulate successfully." It is generally accepted that in brachyurans maturity in some females cannot be determined from the condition of the gonads because development and ovulation often occur a considerable time after mating.

In the case of red crabs, several criteria were examined in an effort to define the size (age) at which females mature. These included the size distribution of ovigerous and nonovigerous females, the incidence of physical indicators of copulation, and changes in the features of the vulvae and abdomen.

Ovigerous Females

The size-frequency distribution of 755 females captured in November 1974, September 1975, and January 1976 reveals the incidence of ovigerous individuals and those with egg remnants on the pleopods (Figure 6). In November and September, 27.3% and 15.7%, respectively, of females ≥71 mm CL (97 mm CW) were ovigerous; 9.0% of females ≥71 mm in September carried egg remnants. In January, 25.5% of females ≥71 mm CL were berried; two of these showed some evidence of egg hatching. Most (94%) of the ovigerous individuals and those with egg remnants were between 71 and 113 mm CL (97-131 mm CW); only four crabs were smaller.

Physical Evidence of Copulation

In numerous species of crabs, recent copulation by the female is indicated by the presence of a hardened mass of spermatozoa and associated secretions protruding from the vulvae (Hartnoll 1969). This so-called sperm plug does not occur in *Geryon quinquedens*.

The exoskeletons of red crabs that have not recently molted are blackened or discolored in abraded or damaged areas and are usually infested with lepadid barnacles *Trilasmis* sp. The association of lepadids and discoloration serves as an indicator of a time lapse since the last molt, although the exact length of time cannot presently be determined. It was reasoned that abrasion and damage of vulval margins due to copulation would result in similar discoloration. This was verified

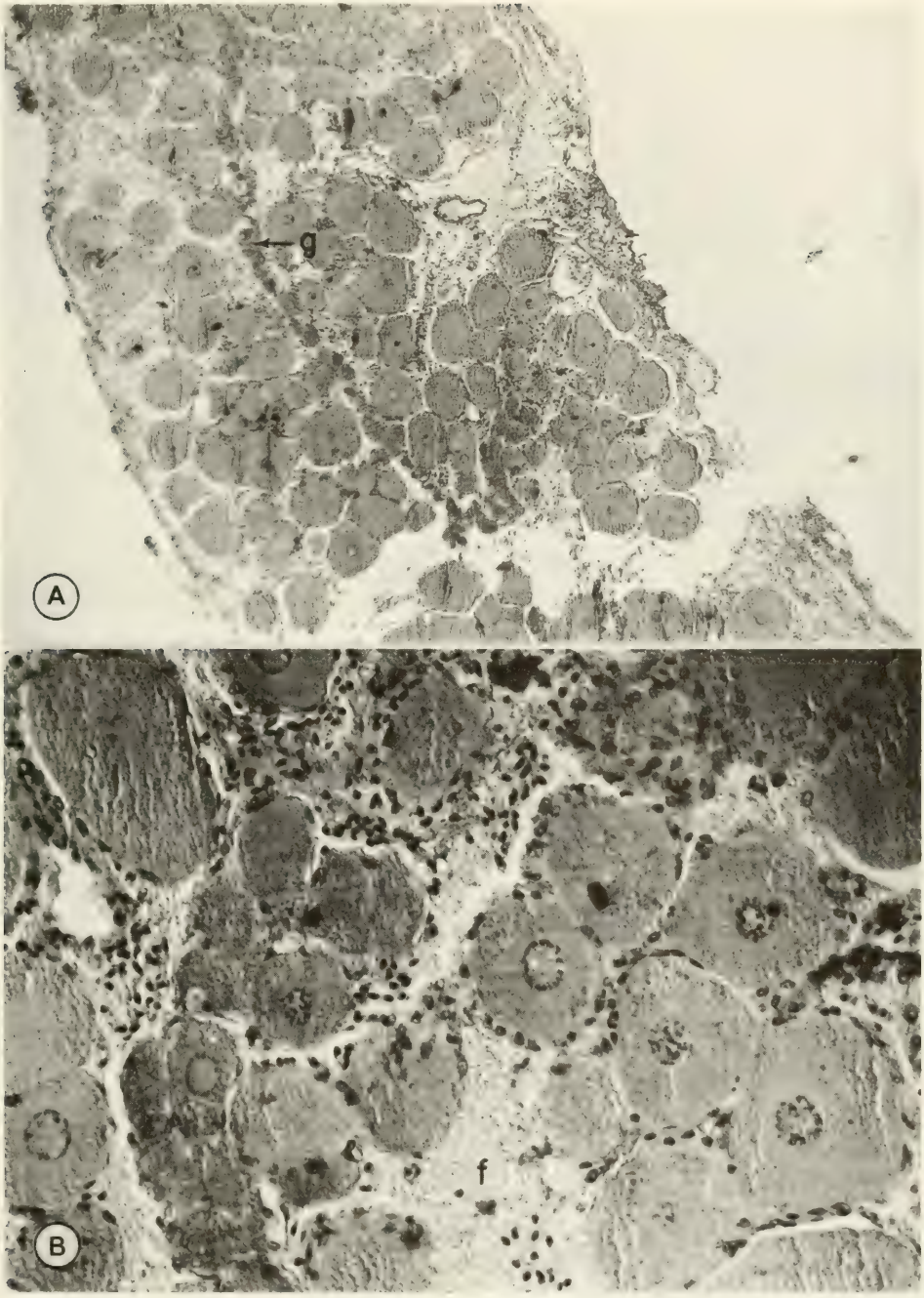


FIGURE 4.—Redeveloping ovary of *Geryon quinquedens* from ovigerous crab. A. 25×. Germinative zone (g) and developing ova are evident. B. Higher magnification (125×) showing prevalence of fibrous connective tissue (f) among various sizes of developing ova.

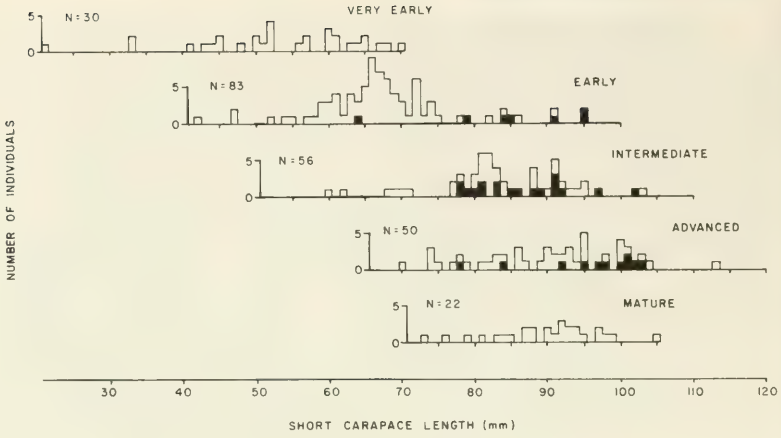


FIGURE 5.—Distribution of female *Geryon quinquedens* according to size (carapace length) and stage of ovarian development. November 1974 and September 1975 samples pooled. Black areas indicate ovigerous crabs and those with egg remnants on pleopods.

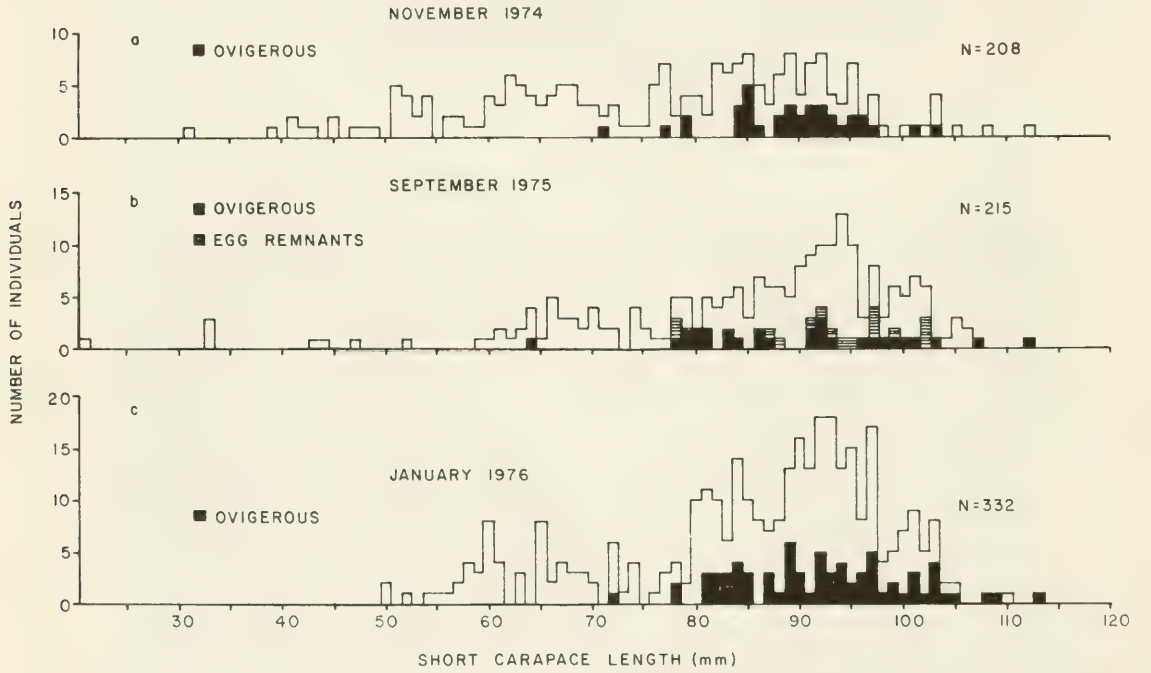


FIGURE 6.—Size-frequency distribution of female *Greyon quinquedens* captured in November 1974 (a), September 1975 (b), and January 1976 (c). Ovigerous individuals are indicated in black; those with egg remnants on pleopods by horizontal stripes.

by examining the spermathecal contents of 67 crabs with discolored vulvae (14 with extruded eggs, egg remnants, or damaged pleopods and 53 with clean, intact pleopods). Eleven (79%) of the recently ovulated females (78-103 mm CL) and 47 (89%) females with clean pleopods (45-105 mm CL) contained sperm (Figure 7). Twenty-one crabs (50-75 mm CL) with immature vulvae were similarly examined; none had sperm in the spermathecae. Another 17 crabs (50-72 mm CL) with immature vulvae were not examined for the presence of sperm because the spermathecae were undeveloped; only the tubular vagina was present between the ovary and gonopore.

Blackened vulval margins may be used as a criterion to indicate that copulation of the female crab has occurred, if other obvious signs (eggs or remnants) are absent. The 89% incidence among nonovigerous females supports this contention. The 79% incidence among ovulated females is low,

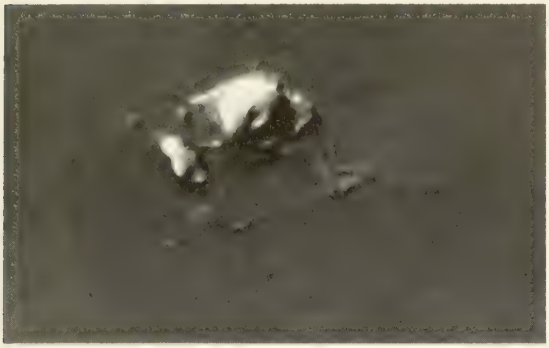


FIGURE 7.—Isolated sperm from spermatheca of 83-mm CL *Geryon quinquedens*. Nonmobile processes extend from nuclear region surrounding a central, refringent structure, most likely the acrosome (Brown 1966). Interference microscopy, 1300×.

but expected. None of these crabs had swollen or turgid spermathecae of the type shown in Figure 1. In most cases, only residual quantities of seminal secretions were present in the receptacles, indicating that most of the deposit had been used in past ovulation(s) or absorbed.

The presence of discolored vulval margins among large crabs suggested that they may provide a physical criterion for copulation, similar to those demonstrated for other brachyurans (Veillet 1945; Butler 1960; Hartnoll 1969). Vulval margins of 93.5% of the females ≥70 mm CL examined (n = 328) were blackened (Figure 8). All females <70 mm CL had vulvae with intact margins. Not included in Figure 8 are an unusually small inseminated female (47 mm CL) and the ovigerous 64-mm CL specimen included in Figure 6b.

One crab (47 mm CL) with small (1.2 mm long), but open, mature-type vulva was sperm positive. This unusually small crab had obviously mated but the vulval margins were not blackened. It is physically possible for a female this small to mate with a male of similar size. I have observed morphologically functional pleopods, with penis inserted in the first pair, on male crabs as small as 38 mm CL. The size at which males become physiologically mature is not known, but it must be relatively small.

Change in Vulvae

Although variable in form, vulvae of *G. quinquedens* undergo a recognizable growth and development pattern which parallels growth in body size and ovarian development. Six types are recognized (Figure 9). The first form vulvae (a) are slitlike and tightly closed. The observed size range appears to be related to crab length (Table 2). Form (b) vulvae are recurved, closed, and slightly larger than the longest form (a) vulvae. Forms (c) and (d), irregularly shaped and partially open, range from a size comparable to the largest vulvae of type (a) to that of type (e). Unusually large (d) vulvae (2.6 mm) were observed in a 78-mm CL crab. Form (e) vulvae are oval, gaping, and appear to immediately precede the mature vulva. Form (f) is the enlarged (2.4-3.9 mm), gaping, and usually blackened vulvae of the larger, mated crabs.

TABLE 2.—Incidence of vulval type and size range in relation to carapace length of female *Geryon quinquedens*.

Type	n	Carapace length (mm)	n	Vulval length range (mm)
a	4	20-33	4	0.2-0.3
	10	57-66	10	0.6-0.9
b	5	56-60	0	no data
	15	61-74	8	0.7-1.2
c	9	50-60	5	0.5-0.8
	17	61-74	13	0.8-1.5
d	6	61-72	6	0.7-1.3
	1	78	1	2.6
e	3	47-60	3	0.6-1.2
	9	61-72	7	0.8-1.2
f	1	45	1	3.0
	51	70-103	12	2.4-3.9

Change in Abdomen Width

The abdomen width (Y) to carapace length (X) relationship is allometric and is transformed to a straight line by the equation:

$$\log Y = -0.875 + 1.321 \log X, n = 251; r = 0.990$$

The relationship changes in the 60- to 75-mm CL range (Figure 10) so linear regressions were calculated separately for crabs with mature (f) vulvae:

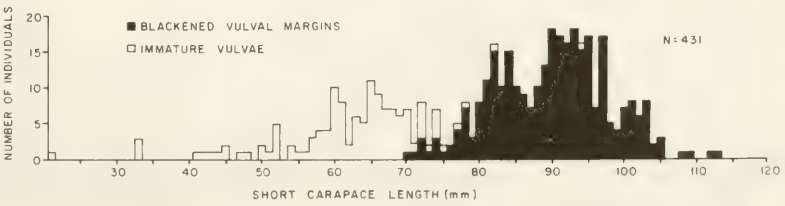


FIGURE 8.—Size-frequency distribution of female *Geryon quinquedens* with immature gonopores (white) and with discolored gonopore margins (black). November 1974, September 1975, and January 1976 collections pooled.

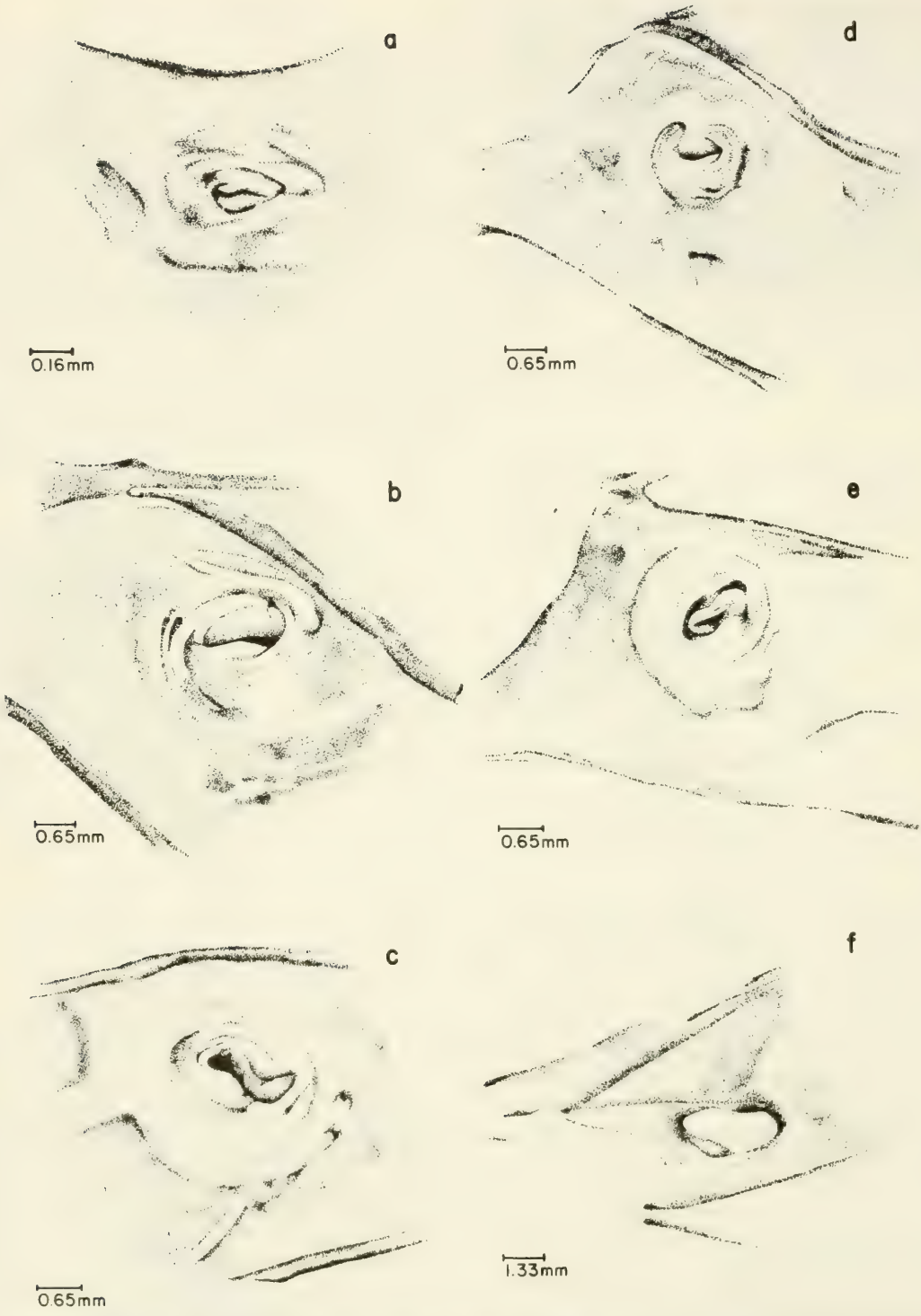


FIGURE 9.—Structural variation in vulvae of female *Geryon quinquedens*. Portions of thoracic sternites V, VI, VII illustrated. a. First form, slitlike, from 20-mm CL crab. b. Recurved, closed, 66 mm CL. c and d. Irregular shape, partially open, 74-mm and 71-mm CL crabs, respectively. e. Oval, gaping, 68 mm CL. f. Oval, enlarged, with blackened margins, 90 mm CL.

$$Y = -8.286 + 0.662X, n = 160; r = 0.943$$

and those with immature vulvae:

$$Y = -8.512 + 0.641X, n = 91; r = 0.971.$$

The size range in which relative growth of the fifth abdominal segment changes is clearly associated with the maturation of the vulvae, copulation and insemination, gonad development, and extrusion of eggs. Females become sexually mature within the intermolt size range 65-75 mm CL (80-91 mm CW). Most intermolt females ≥76 mm CL show signs of copulation and insemination, and their ovaries are in intermediate to advanced stages of development. Few females <75 mm CL are ovigerous.

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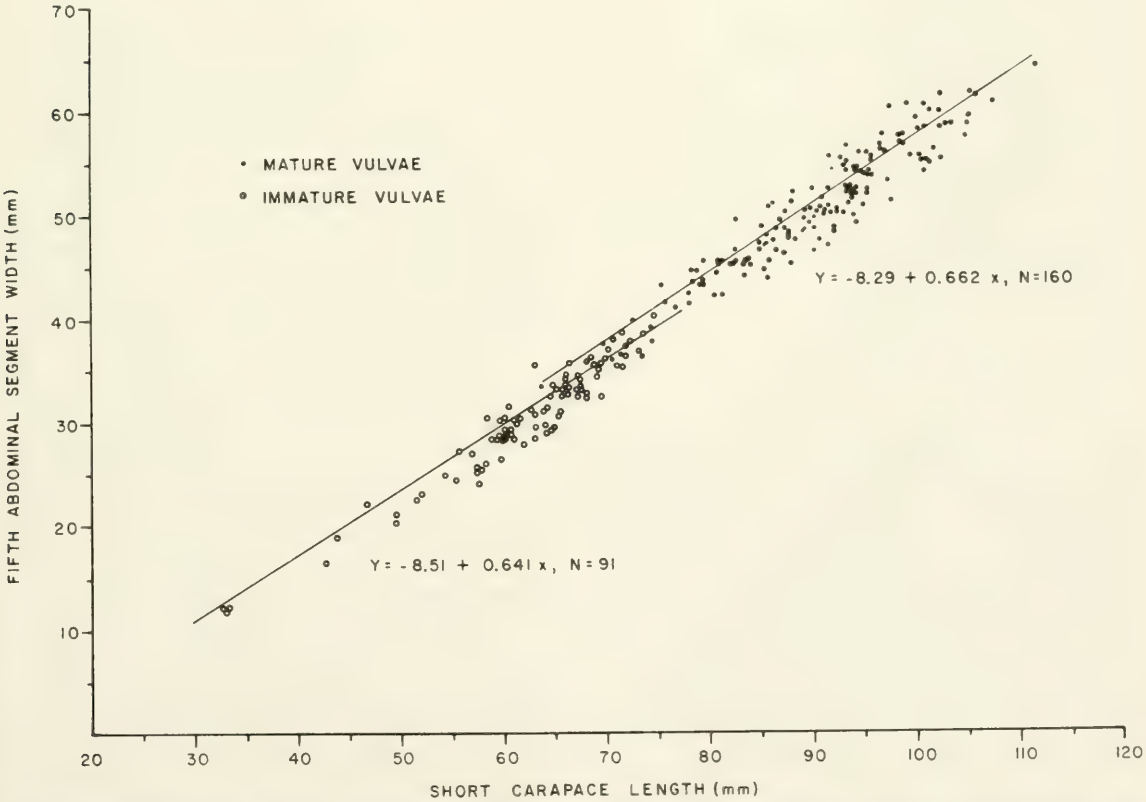

FIGURE 10.—Relationship of width of fifth abdominal segment to short carapace length for *Geryon quinquedens* with mature (dots) and immature vulvae (circles).

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COMPARISONS OF CATCHES OF FISHES IN GILL NETS IN RELATION TO WEBBING MATERIAL, TIME OF DAY, AND WATER DEPTH IN ST. ANDREW BAY, FLORIDA

PAUL J. PRISTAS AND LEE TRENT[1]

ABSTRACT

Monofilament and multifilament gill nets were fished simultaneously in shallow- (0.7-1.1 m), mid- (2.2-2.6 m), and deep- (5.2-5.6 m) water zones for 40 days between 19 September and 29 December 1972, in lower St. Andrew Bay, Fla. Each net was 33.3 m long, had stretched mesh of 9.5 cm, extended from water surface to bottom, and was anchored in position. Nets were checked at sunrise and sunset. Fifty-two species of fishes and one hybrid from 30 families were caught. The 12 most abundant species composed 92% of the total number (4,066) caught. Catch comparisons between 1) webbing materials, 2) times of day, and 3) water depths were made from data on catches of the 12 most abundant species. Catches in monofilament webbing were greater than those in multifilament webbing for 8 of the 12 species. Greater catches were made at night for all 12 species. Catches of eight species were highest in the deep-water zone, but catches of the remaining four species were highest in the shallow-water zone. Monofilament nets were damaged least, and percent damage decreased as depth zones increased.

The National Marine Fisheries Service (NMFS) began collecting a variety of fishes from coastal and offshore waters throughout the United States in 1972 for heavy-metal analyses. Each coastal laboratory of NMFS was responsible for the fish collections in their respective geographic area, and we at the Panama City Laboratory were to collect relatively large numbers of about 15 species. We decided that set gill nets would be our most effective sampling gear but could find no published information on their effectiveness in Gulf of Mexico estuaries in relation to various efficiency factors such as twine size, mesh size, and location and time of day to set the nets.

The literature did reveal that gill nets are among the most important types of fishing gear used in Florida. Over 34.6 million pounds of finfish, valued at over $4.7 million to the fishermen, were caught with gill and trammel nets on the west coast of Florida in 1971 (National Marine Fisheries Service 1974). Set gill nets, the type used in this study, are not commercially used to any extent in Florida estuaries except for spotted seatrout, *Cynoscion nebulosus,* and even in this fishery the nets are left in the water for only about 2 h (Siebenaler 1955). Information about the efficiency of set gill nets in the gulf was limited to comparisons of catches of king mackerel, *Scomberomorus cavalla,* and Spanish mackerel, *S. maculatus,* between monofilament and multifilament gill nets (Mihara et al. 1971).

We decided to capture the fishes needed for the heavy-metal survey in such a way that information could be generated on the efficiency of gill nets in our area. The objectives of this study were: 1) to compare gill net catches in an estuarine system in relation to webbing materials, times of day, and depth zones; and 2) to estimate net damage in relation to webbing materials and depth zones.

STUDY AREA AND METHODS

The St. Andrew Bay system, located between long. 85°23′ and 85°53′W and lat. 30°00′ and 30°20′N along the northwest Florida coast, covers about 280 km² (McNulty et al. 1972). Physical, hydrological, and sedimentological characteristics of the bay system have been presented by Hopkins (1966), Ichiye and Jones (1961), and Waller (1961). Tidal fluctuations in the bay average about 0.4 m (National Ocean Survey 1971).

The study area was located 0.6 km northwest of the western entrance into St. Andrew Bay. Depths at the net locations at mean low tide were 0.7-1.1 m (shallow), 2.2-2.6 m (mid), and 5.2-5.6 m (deep). During the study, surface temperatures and salinities ranged from 11.4° to 27.0°C and 25.3 to 34.6‰, respectively (determined with a

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Beckman[2] RS5-3 salinometer), and turbidities ranged from 0.2 to 2.8 Formazin turbidity units (determined with a Hach turbidimeter). Substrate was similar to the sand regime (greater than 80% sand) described by Waller (1961). Submergent vegetation was dense in the shallow zone, less dense in the mid zone, and sparse in the deep zone and consisted primarily of turtle grass, *Thalassia testudinum;* shoal grass, *Diplanthera wrightii;* and manatee grass, *Syringodium filiforme.* At least 70 species of fishes and sharks were caught by gill nets in 1973 in the immediate vicinity of the study area (May et al. 1976; Pristas and Trent[3]).

The gill nets were constructed of either #208 monofilament webbing (transparent; 0.52-mm strand diameter) or #220 multifilament webbing (white; 0.64-mm strand diameter). The 9.5-cm (3¾-inch) stretched mesh webbing was hung on the half basis (two lengths of stretched mesh to one length of float line) with the floats spaced 1.5 m apart. The nets were 33.3 m long and either 1.5, 3.0, or 6.1 m deep. Nets were held in position by bridle lines attached to anchors.

One monofilament and one multifilament gill net were set in each depth zone and were about 50 m apart. The webbing types were randomly assigned to the two net locations each time the nets were set. The nets were fished during eight periods from 19 September to 29 December 1972 (Table 1) and were set and pulled within ±1 h of sunset during each period. Nets were fished in a random order and removal of fish from the nets required from 1 to 3 h. Night catches were removed from the nets between 1 h before to 2 h after sunrise, and day catches were removed within ±1 h of sunset; consequently, day and night fishing intervals overlapped slightly.

Wilcoxon's signed rank test, a nonparametric procedure, was used statistically to compare catch per net between day and night and between monofilament and multifilament samples. For these comparisons the number of fish of a species caught in a single net, categorized by webbing type, depth zone, and day or night was used.

Tukey's *w*-procedure was used statistically to compare catch per net between depth zones. For this procedure, the number of fish of a species caught per net per 24-h period was transformed ($\log_{10}$ number caught + 1) prior to running the comparisons. Comparisons within each webbing type and time of day were not made because of insufficient data. Both testing procedures are described by Steel and Torrie (1960).

In our comparisons between depth zones a question arose as to whether the catches should be adjusted for the unequal amounts of webbing fished among depths, i.e., the 1.5-m nets had half and a fourth as much webbing as the 3.0- and 6.1-m nets, respectively. We did not adjust values, because we were interested in the number of fish passing over an area of bay bottom per unit time (i.e., the depth at which the most fish could be caught) rather than the number of fish passing through a unit volume of water per unit time. On this basis we did not need to adjust catches among depths, because each net blocked the same horizontal distance of the water column.

Intermittently, the nets were inspected for damage. Damaged areas never exceeded 8% of the total net area before the netting was repaired or replaced.

RESULTS

During the study, 4,066 fish representing 30 families, 52 species, and 1 hybrid were caught. We decided that catches of only the 12 most abundant species provided sufficient data for comparison. These 12 species composed 92% of the total catch (Table 1). Of the 12 species, 4 (bluefish, *Pomatomus saltatrix;* Spanish mackerel, *Scomberomorus maculatus;* Atlantic croaker, *Micropogon undulatus;* striped mullet, *Mugil cephalus*) are considered important locally as recreational and food fishes. The other eight species were: Gulf menhaden, *Brevoortia patronus;* sea catfish, *Arius felis;* yellowfin menhaden, *B. smithi;* little tunny, *Euthynnus alletteratus;* Atlantic sharpnose shark, *Rhizoprionodon terraenovae;* gafftopsail catfish, *Bagre marinus;* hybrid menhaden, *Brevoortia patronus* × *B. smithi* (Reintjes 1969); and pinfish, *Lagodon rhomboides.*

Comparisons Between Webbing Materials

Differences in catch per net between webbing materials varied in relation to species, time of day, and depth zone. Combined (times of day and depths) mean catches in monofilament webbing were significantly greater than those in multifilament webbing for Gulf menhaden, bluefish,

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3]Pristas, P. J., and L. Trent. 1976. Seasonal abundance, size, and sex ratio of fishes caught with gill nets in St. Andrew Bay, Florida. (Unpubl. manuscr.)

TABLE 1.—Catches (number caught per 24-h period) of the 12 most abundant species in St. Andrew Bay, Fla., 1972.

Date	Gulf menhaden	Sea catfish	Bluefish	Yellowfin menhaden	Little tunny	Atlantic sharpnose shark	Spanish mackerel	Atlantic croaker	Gafftopsail catfish	Hybrid menhaden	Striped mullet	Pinfish	Total number caught
20 Sept.	7	11	10	0	0	0	12	0	11	0	0	0	51
21	7	3	7	0	1	0	13	0	9	0	0	1	41
22	2	2	6	0	0	2	3	0	9	0	0	0	24
6 Oct.	6	5	7	0	10	1	7	9	5	0	5	1	56
7	1	2	11	0	0	1	1	6	3	0	0	0	25
8	19	3	14	0	0	1	2	11	3	0	2	0	55
9	16	6	5	0	0	1	4	8	2	0	1	0	43
10	0	2	3	0	0	0	3	3	2	0	0	0	13
11	5	8	27	0	0	0	4	20	3	0	0	2	69
12	3	4	9	0	1	3	2	48	4	0	2	1	77
13	1	4	1	0	0	0	31	23	4	0	0	0	64
14	1	7	7	0	6	3	43	7	2	0	4	0	80
15	1	4	5	0	0	0	4	3	5	0	1	3	26
16	0	3	1	0	14	2	14	4	3	0	0	2	43
17	4	6	7	0	5	1	0	9	2	0	0	0	34
18	13	5	0	0	0	1	2	7	4	0	1	0	33
19	5	3	2	0	9	0	8	3	3	0	0	0	33
1 Nov.	35	7	9	0	32	4	3	6	1	0	0	5	102
2	184	35	9	0	8	5	3	1	5	0	4	7	261
3	147	9	0	3	20	12	1	0	8	0	0	2	202
4	314	9	5	0	4	0	2	0	23	0	0	4	361
6	9	11	6	0	6	1	4	3	2	0	1	5	48
7	61	18	16	0	9	9	5	2	10	6	0	4	140
8	108	20	26	2	29	57	5	2	23	1	10	6	289
9	131	19	3	2	5	43	10	3	11	1	0	5	233
10	1	6	1	0	0	16	2	0	2	0	0	5	33
14	35	5	4	3	12	40	4	0	3	0	32	2	140
15	43	5	14	148	45	19	2	0	4	66	20	7	373
16	136	43	10	35	6	6	6	0	5	11	0	6	264
17	32	46	25	10	21	8	1	1	5	0	0	1	150
29	43	7	11	17	0	0	0	0	0	0	0	0	78
30	50	4	2	21	1	0	0	0	0	3	0	0	81
1 Dec.	28	2	2	2	0	0	0	1	0	2	0	0	37
12	0	11	1	1	1	0	0	0	0	1	0	0	15
13	3	22	1	12	0	0	0	0	0	1	0	0	39
14	33	20	0	1	2	0	0	0	0	0	0	0	56
15	4	19	1	2	5	0	0	0	0	0	0	0	31
27	8	2	0	1	0	0	0	0	0	0	0	0	11
28	12	2	0	0	0	0	0	0	0	0	0	0	14
29	13	0	0	0	0	0	0	0	0	0	0	0	13
Total	1,521	400	268	260	252	236	201	180	176	92	83	69	3,738

Spanish mackerel, Atlantic croaker, and striped mullet (Table 2). When catches of each of these five species were analyzed separately by time of day and depth, those differences which were significant showed greater catches again in the monofilament webbing. These results for Spanish mackerel are similar to those reported by Mihara et al. (1971), who found monofilament webbing more efficient than multifilament webbing on Spanish mackerel.

Significant differences between webbing materials were not found for combined mean catches of the remaining seven species, but were found for catches of four of these species (sea catfish, Atlantic sharpnose shark, gafftopsail catfish, and pinfish) during the night at one or more depths. Catches of sea catfish were significantly greater in multifilament webbing at middepth. Catches of Atlantic sharpnose sharks were significantly greater in monofilament in the deep zone, and in multifilament in the mid zone. Significantly more gafftopsail catfish were caught in multifilament webbing in the mid zone as were pinfish in multifilament webbing in the mid zone, and in monofilament in the shallow zone.

Comparisons Between Times of Day

Combined (webbing types and depths) mean catches of all 12 species were significantly greater at night than during the day (Table 3). When catches were analyzed separately by webbing materials and depths, the significant differences again revealed that more fish of each species were caught at night.

Comparisons Between Depth Zones

Catches of 10 of the 12 species were significantly different among depths (Table 4). Of the ten, Gulf

TABLE 2.—Statistical comparisons between mean catches from monofilament ($\bar{X}$) and multifilament ($\bar{Y}$) webbing. Dashes (—) indicate no data.

	Times of day and depths combined				Day												Night											
					Shallow				Mid				Deep				Shallow				Mid				Deep			
Species	$\bar{X}$	$\bar{Y}$	df	t or z	$\bar{X}$	$\bar{Y}$	df	t	$\bar{X}$	$\bar{Y}$	df	t	$\bar{X}$	$\bar{Y}$	df	t	$\bar{X}$	$\bar{Y}$	df	t or z	$\bar{X}$	$\bar{Y}$	df	t or z	$\bar{X}$	$\bar{Y}$	df	t or z
Gulf menhaden	9.3	6.4	97	4.2*	1.0	0.0	1	—	1.5	0.5	4	—	2.4	3.4	5	—	2.3	1.7	28	1.8**	11.0	3.8	29	3.5*	16.8	14.7	30	1.3
Sea catfish	1.7	2.0	106	0.9	0.5	0.5	2	—	0.8	0.2	5	—	0.9	1.2	15	51.5	2.8	2.4	24	83.0	1.1	2.0	25	85.5**	1.9	2.5	35	0.7
Bluefish	2.2	1.6	69	1.7**	0.8	0.2	5	—	1.0	0.4	8	7.0	0.0	1.0	1	—	2.7	2.1	29	0.6	2.5	1.8	20	57.0	2.0	1.3	6	8.0
Yellowfin menhaden	6.4	2.9	28	0.3	0.0	1.0	1	—	0.0	1.0	1	—	—	—	—	—	3.4	3.1	10	20.0	3.3	4.4	8	11.0	14.7	1.7	8	7.5
Little tunny	2.3	3.1	47	0.8	—	—	—	—	0.7	0.3	3	—	0.0	1.0	1	—	0.3	1.3	6	4.5	2.9	2.7	18	74.0	2.6	4.6	19	51.0
Atlantic sharp-nose shark	2.7	2.4	46	1.2	0.0	1.0	1	—	2.5	1.0	2	—	1.7	0.5	4	—	2.6	2.0	7	10.5	1.5	3.4	16	23.5**	4.5	2.3	16	24.0**
Spanish mackerel	2.1	0.4	79	5.1*	1.0	0.1	9	0.0*	1.9	0.1	13	0.0*	4.4	0.2	10	6.0**	1.2	0.5	13	16.5**	2.0	0.5	19	24.0*	2.3	1.1	15	43.0
Atlantic croaker	2.9	0.8	48	4.6*	2.4	0.3	7	5.0	1.0	0.0	1	—	—	—	—	—	4.6	1.5	21	6.0*	1.5	0.2	11	7.0**	1.3	0.5	8	8.0
Gafftopsail catfish	1.6	1.8	43	0.4	—	—	—	—	0.5	0.5	2	—	0.3	0.7	6	7.0	1.0	0.0	1	—	0.6	1.7	15	20.0**	2.4	2.1	19	116.0
Hybrid menhaden	3.3	2.8	15	48.0	—	—	—	—	—	—	—	—	0.0	1.0	1	—	2.4	2.6	5	—	2.2	2.7	6	6.0	8.3	4.0	3	—
Striped mullet	3.7	1.5	16	16.5*	1.4	0.2	5	—	2.0	0.0	1	—	—	—	—	—	5.0	2.3	10	10.0	—	—	—	—	—	—	—	—
Pinfish	0.8	1.1	37	0.5	0.8	0.7	6	—	0.2	1.5	6	2.5	—	—	—	—	1.5	0.5	13	6.0*	0.4	1.7	10	6.0**	0.0	1.0	2	—

*Significant at 1% level.
**Significant at 5% level.

TABLE 3.—Statistical comparisons between mean catches from night ($\bar{X}$) and day ($\bar{Y}$). Dashes (—) indicate no data.

	Webbing types and depths combined				Monofilament												Multifilament											
					Shallow				Mid				Deep				Shallow				Mid				Deep			
Species	$\bar{X}$	$\bar{Y}$	df	t or z	$\bar{X}$	$\bar{Y}$	df	t	$\bar{X}$	$\bar{Y}$	df	t or z	$\bar{X}$	$\bar{Y}$	df	t or z	$\bar{X}$	$\bar{Y}$	df	t	$\bar{X}$	$\bar{Y}$	df	t	$\bar{X}$	$\bar{Y}$	df	t
Gulf menhaden	8.8	0.3	131	9.9*	2.9	0.0	22	5.0*	9.1	0.2	26	4.5*	13.2	0.4	29	4.7*	3.0	0.0	16	0.0*	5.4	0.1	18	0.0*	16.1	0.8	20	0.0*
Sea catfish	3.0	0.3	112	8.9*	3.7	0.1	18	0.0*	1.5	0.2	17	11.0*	2.9	0.6	23	13.0*	2.8	0.0	21	0.0*	3.1	0.1	15	0.0*	4.3	0.9	18	0.0*
Bluefish	2.8	0.2	85	7.4*	3.1	0.2	24	10.0*	2.7	0.4	19	11.0*	3.0	0.0	3	—	2.9	0.1	20	5.0*	2.4	0.2	16	15.0*	2.0	0.3	3	—
Yellowfin menhaden	6.1	0.0	40	5.4*	4.3	0.0	8	0.0*	4.3	0.0	5	—	16.9	0.0	6	0.0**	3.9	0.1	8	3.0**	4.4	0.1	8	2.5**	2.8	0.0	4	—
Little tunny	4.2	0.1	55	6.4*	2.0	0.0	1	—	4.3	0.2	10	0.0*	3.4	0.0	14	0.0*	1.6	0.0	4	—	4.4	0.1	11	0.0*	5.9	0.1	15	2.5*
Atlantic sharp-nose shark	3.6	0.3	58	6.3*	3.0	0.0	5	—	2.0	0.3	12	10.0**	4.7	0.5	15	7.0**	2.3	0.2	5	—	4.6	0.3	12	0.0*	4.0	0.2	9	0.0*
Spanish mackerel	1.6	1.1	61	2.6*	1.1	0.6	13	27.5	1.8	1.1	18	63.5	2.7	3.7	10	26.5	1.0	0.2	5	—	1.0	0.1	9	4.5**	2.1	0.0	6	0.0**
Atlantic croaker	2.9	0.4	56	6.2*	4.8	0.9	20	0.0*	1.6	0.5	10	7.0**	1.4	0.0	6	0.0*	2.3	0.1	14	4.0*	1.0	0.0	2	—	2.0	0.0	2	—
Gafftopsail catfish	2.3	0.1	56	9.0*	—	—	—	—	0.8	0.2	5	—	2.6	0.1	23	0.1*	—	—	—	—	1.8	0.1	10	0.0*	2.7	0.2	18	0.0*
Hybrid menhaden	4.8	0.1	19	0.0*	3.7	0.0	3	—	2.2	0.0	6	—	25.0	0.0	1	—	3.3	0.0	4	—	16.0	0.0	1	—	3.0	0.3	4	—
Striped mullet	4.3	0.6	16	25.0*	5.0	0.7	9	7.5	0.0	2.0	1	—	—	—	—	—	3.8	0.2	6	—	—	—	—	—	—	—	—	—
Pinfish	1.2	0.5	36	2.4*	1.3	0.5	12	16.0	0.8	0.2	5	—	—	—	—	—	0.9	0.5	8	12.0	1.7	1.0	9	15.5	1.0	0.0	2	—

*Significant at 1% level.
**Significant to 5% level.

TABLE 4.—Statistical comparisons between catches from shallow- (S), mid- (M), and deep- (D) water depth zones.

Species	Depth, mean catch, and significance lines[1]			Error df
	S	M	D	
Gulf menhaden	1.6	6.0	13.5	213
	M	S	D	
Sea catfish	1.0	1.5	2.3	246
	D	M	S	
Bluefish	0.3	1.5	2.2	195
	M	S	D	
Yellowfin menhaden	2.6	2.7	5.5	69
	S	M	D	
Little tunny	0.2	2.5	3.3	123
	S	M	D	
Atlantic sharpnose shark	0.9	2.3	3.1	111
	S	M	D	
Spanish mackerel	0.5	1.1	1.4	198
	D	M	S	
Atlantic croaker	0.3	0.5	3.5	123
	S	M	D	
Gafftopsail catfish	0.0	0.6	2.4	168
	S	M	D	
Hybrid menhaden	1.9	2.2	2.9	36
	D	M	S	
Striped mullet	0.0	0.1	4.3	54
	D	M	S	
Pinfish	0.1	0.9	1.0	102

[1] Any two means not underscored by the same line were significantly different at the 5% level.

menhaden, little tunny, Atlantic sharpnose shark, Spanish mackerel, and gafftopsail catfish were caught in greater numbers as depth increased, and sea catfish were caught in greatest numbers in the deep zone. Conversely, catches decreased with increasing depth for bluefish, Atlantic croaker, striped mullet, and pinfish.

Net Damage

Monofilament nets were damaged less than multifilament nets in each depth zone fished. In terms of the amount of surface area damaged, shallow nets received the least and deep nets the greatest (Table 5). When corrected to percent of total webbing damage in nets at each zone, shallow nets received the greatest proportion of damage. Blue crab, *Callinectes sapidus,* caused damage to both webbing types. Multifilament webbing was damaged the most, possibly because 87% of all blue crabs taken were caught in multifilament webbing.

TABLE 5.—Average daily net damage in square meters and percent of total net area in relation to depth of net and to webbing material.

Depth of net (m)	Monofilament		Multifilament	
	m^2	Percent	m^2	Percent
1.5	0.11	0.21	0.16	0.33
3.0	0.16	0.16	0.23	0.23
6.1	0.31	0.15	0.44	0.22
Average of three nets	0.25	0.16	0.34	0.24

SUMMARY AND DISCUSSION

In this study, catch per net was higher with monofilament than with multifilament gill nets; over 58% of the 12 most abundant species and over 71% of the 4 most abundant food and recreational fishes (bluefish, Spanish mackerel, Atlantic croaker, and striped mullet) were caught in monofilament nets.

Catch per net was much greater at night than during the day; about 93% of the 12 most abundant species and about 82% of the 4 most abundant food fishes were taken at night.

Total catches of the 12 most abundant species were 816 (22%), 1,063 (28%), and 1,859 (50%) fish in the shallow, mid, and deep zones, respectively.

For evaluation where the amount of webbing could be an important cost factor, total catches in each depth zone were converted to catches per unit surface area of webbing by dividing total catches for the shallow, mid, and deep zones by one, two, and four, respectively. Catches per unit area of webbing for the 12 species combined were 816 (45%), 531 (29%), and 465 (26%) fish for the shallow, mid, and deep zones. For the four most abundant species of food fishes unadjusted catches per unit area of net were 407 (56%), 196 (27%), and 126 (17%), and adjusted catches per unit area of net were 407 (76%), 98 (18%), and 32 (6%) fish for the shallow, mid, and deep zones. Thus, on either basis, fishing in the shallow zone was the most productive.

Other factors of importance in this study in terms of overall efficiency included net damage, ease of fishing, cost, and storage of webbing. Daily average net damage was 0.16% for monofilament and 0.24% for multifilament webbing. Fish could be removed faster and fewer crabs were caught in monofilament nets. Monofilament nets tangled less and were set and retrieved faster than multifilament nets. Disadvantages of monofilament compared to multifilament nets were: greater cost per pound (almost double); more storage room required; and greater difficulty of repairing the webbing owing to the requirement of double knots to prevent slippage.

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AGE DETERMINATION, REPRODUCTION, AND POPULATION DYNAMICS OF THE ATLANTIC CROAKER, *MICROPOGONIAS UNDULATUS*[1, 2]

MICHAEL L. WHITE AND MARK E. CHITTENDEN, JR.[3]

ABSTRACT

A validated scale method of age determination is described for the Atlantic croaker, *Micropogonias undulatus*. Two age-classes were usually observed, but only one was abundant. Mean total lengths were 155-165 mm at age I and 270-280 mm at age II based on three methods of growth estimation. Fish matured near the end of their first year of life when they were about 140-170 mm total length. Spawning occurred from at least September through March but there was a distinct peak about October. Somatic weight-length relationships varied monthly, and changes appeared to be associated with maturation and spawning. Somatic weight reached a maximum in June, and the minimum was observed in March. Maximum somatic weight loss (24%) occurred in March, but no data were obtained from December through February. In estuaries, age 0 croaker apparently occupied soft-substrate habitat and older fish occurred near oyster reefs. Life spans were only 1 or 2 yr, and the total annual mortality rate was 96%. The above life history pattern appears similar for croaker found throughout the Carolinian Province. Contrasts are presented to illustrate differences in the life histories and population dynamics of croaker found north and south of Cape Hatteras, N.C. A parallel is drawn with apparently similar changes in the American shad, *Alosa sapidissima*, and the suggestion is made that changes in the population dynamics of species that traverse the Cape Hatteras area may represent a general phenomenon.

The Atlantic croaker, *Micropogonias undulatus* (Linnaeus), ranges in the western Atlantic from the Gulf of Maine to Argentina (Chao 1976). It is potentially a very important protein source because it is one of the most abundant inshore fishes of the northern Gulf of Mexico (Gunter 1938, 1945; Moore et al. 1970; Franks et al. 1972) and the Atlantic Ocean off the southeastern United States (Haven 1957; Bearden 1964; Anderson 1968).

Much work has been done on this species. However, many aspects of its life history and population dynamics are not clear; because no reliable method of age determination exists, and reproduction has not been studied intensively. A few early workers, including Welsh and Breder (1924) and Wallace (1940), attempted to age croaker using scales; but criteria for marks were not described and methods were not validated. More recent workers, in general, have not attempted to use hard parts to determine croaker age and growth. The scale method is difficult to apply to croaker (Joseph 1972), and this may be related to its migratory habits and extended spawning season (Suttkus 1955). Only Wallace (1940) studied reproduction using a large series of gonads. However, he worked north of Cape Hatteras, N.C. The life history of croaker found north of Cape Hatteras seems quite different from that of individuals in the Carolinian Province. Studies of reproduction in croaker found south of Cape Hatteras have been based on few fish (Gunter 1945; Bearden 1964) or fish less than 200 mm long (Hansen 1969).

This paper describes a validated method of age determination for croaker, their weight-length and girth-length relationships, habitat segregation between age-groups, spawning seasonality, somatic weight variation, growth, maximum size, life span, and total annual mortality rates. Finally, it contrasts the life histories of croaker found north and south of Cape Hatteras. Geographically, statements made herein apply to the Carolinian Province and/or more northerly waters. With modifications, particularly ones due to calendar differences in seasons, our findings may also apply in the southern hemisphere; but further work is needed there.

MATERIALS AND METHODS

Collections were made from commercial shrimp trawlers during 1974 in the Gulf of Mexico off

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Freeport-Galveston and Port Aransas, Tex., and Cameron, La. Fish were also collected by trawling in Palacios, Galveston, and Matagorda bays, Tex., and Calcasieu Lake, La. Additional fish, hereinafter termed reef fish, were captured by angling with dead shrimp bait (about 25 mm long) near an oyster bar in Galveston Bay. Collection months are indicated in Figure 1.

A sample was taken from each trawl catch by shoveling into a 25-liter container small portions of the catch from various areas of the deck. Unusually large fish were arbitrarily selected to obtain older fish to develop an ageing technique. Total length was measured on each croaker. Total and gonad weights and girth at the origin of the dorsal fin were determined for fish over a broad size range during each sampling period. Scales below the lateral line posterior to the pectoral fin were removed from 1,123 fish, were pressed on plastic slides, and were examined using a scale projector. Scales were examined from small numbers of croaker collected off Mississippi and Fort Pierce, Fla., and in Chesapeake Bay, Va., to judge whether or not the method of age determination proposed herein is valid throughout their range in the Carolinian Province and more northerly waters. The size and appearance of the gonads of more than 1,700 fish were examined, and ovaries were classified following Nikolsky (1963) as summarized by Bagenal and Braum (1971) except that the immature and resting stages were combined.

The regressions of somatic, gonad, and total weights, and girth on total length were computed to express the best linear or quadratic fit using the Statistical Analysis System (Service 1972). Sex data were pooled to compute total weight-length, somatic weight-length, and girth-length regressions, because F tests (Ostle 1963:204) indicated that pooled regression lines were appropriate.

SPAWNING

Spawning occurred over a protracted period extending at least from September to late March, but there was a distinct peak about October. The regressions of gonad weight on length were not significant during May, June, or July for either sex. The mean gonad weight in this period was 0.10 g, and its 95% confidence limits were 0.09-0.11 g. The regressions of gonad weight on length (Figure 2) indicate that gonad development in each sex began by late August, increased greatly during September, reached a peak in October, declined greatly by November, and was at the latter level in March. Similarly, the coefficients of determination (r^2) of the regression lines (Table 1) show that gonad weight variation in each sex was increasingly associated with length until October and then greatly declined. Therefore, it appears that peak spawning occurred in October. Fish captured in the Gulf and by the reef were in all stages of development during September, as were trawl-caught bay fish in October (Figure 3). Therefore, spawning apparently began at least by late September, and some individuals finished or had nearly finished spawning then. Most spawning occurred during October in agreement with the gonad weight-length analyses, because most fish captured in the Gulf were still immature in September. Most fish captured near the reef and in the Gulf were ripe or spent during October and November. Specimens captured in the Gulf during late March were in a resting stage or nearly spent, so that spawning is apparently completed by late March except by a few individuals.

Croaker started to mature at about 140-170 mm total length. Extrapolated x-intercepts or inflection points of the regressions of gonad weight on total length occur in that size range for each sex (Figure 2). Developing fish as small as 136 mm were observed.

Many aspects of croaker spawning appear similar throughout the Carolinian Province. The prolonged spawning period suggested by our data is consistent with frequently reported collections of fish about 25-40 mm long from October to June (many references including Suttkus 1955; Bearden 1964; Hansen 1969; Parker 1971; Swingle 1971; Christmas and Waller 1973; Hoese 1973). The apparent peak of spawning after September agrees with Pearson (1929), Hildebrand and Cable

TABLE 1.—Analyses for the regressions of gonad weight (Y) in grams on total length (X) in millimeters for each sex and month. All regressions were significant at $\alpha = 0.0001$.

Sex	Month	Sample size	r^2	Equation
Males	August	67	0.46	$Y = -0.389 + 0.004X$
	September	108	0.68	$Y = -4.737 + 0.033X$
	October	64	0.73	$Y = -8.804 + 0.055X$
	November	46	0.32	$Y = -2.782 + 0.018X$
	March	35	0.43	$Y = -3.785 + 0.021X$
Females	August	92	0.47	$Y = -0.426 + 0.004X$
	September	286	0.63	$Y = -11.920 + 0.080X$
	October	154	0.67	$Y = -27.135 + 0.177X$
	November	69	0.28	$Y = -15.570 + 0.097X$
	March	41	0.32	$Y = -13.359 + 0.077X$

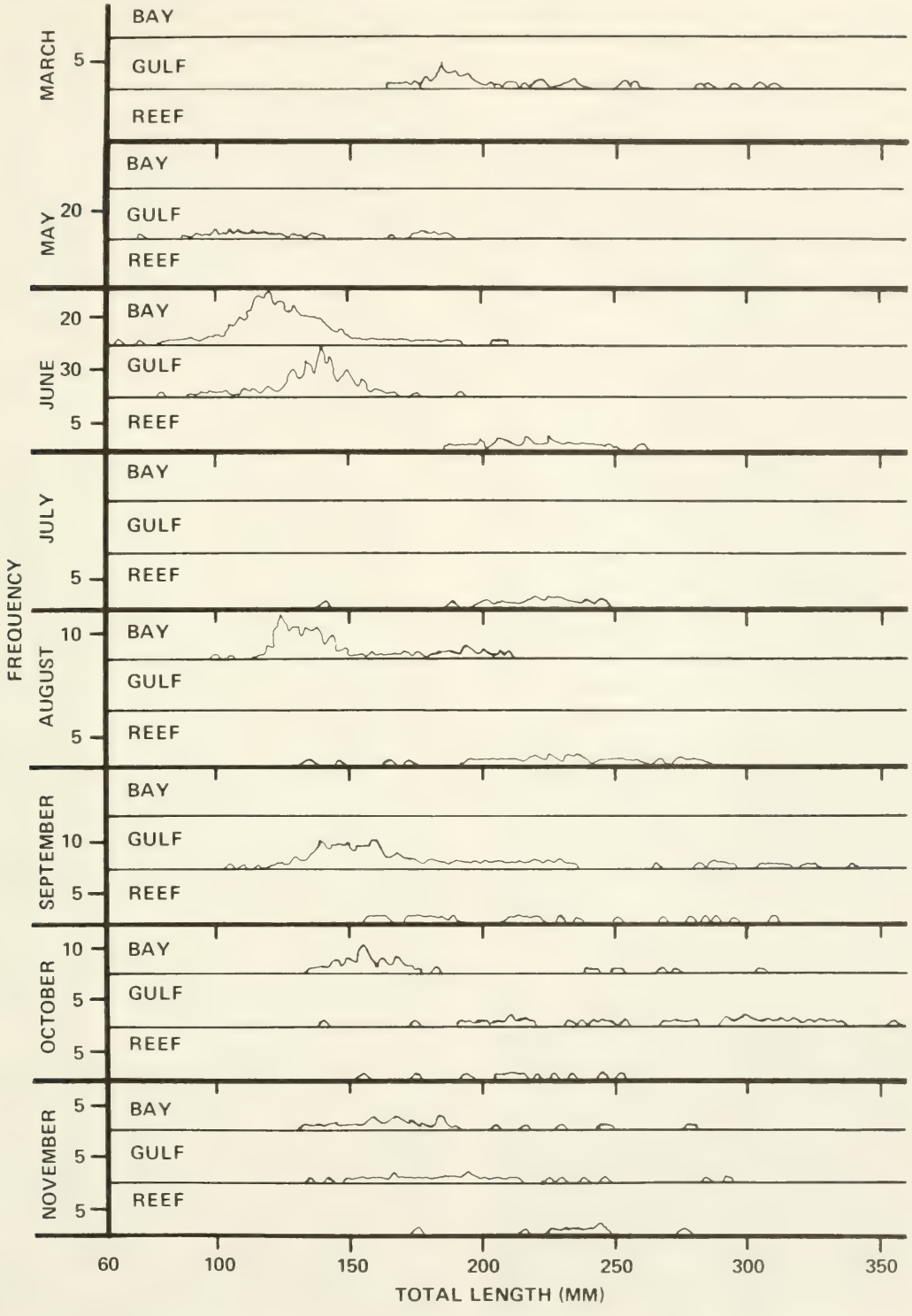

FIGURE 1.—Length frequencies of Atlantic croaker in each area each month. Frequencies are moving averages of three.

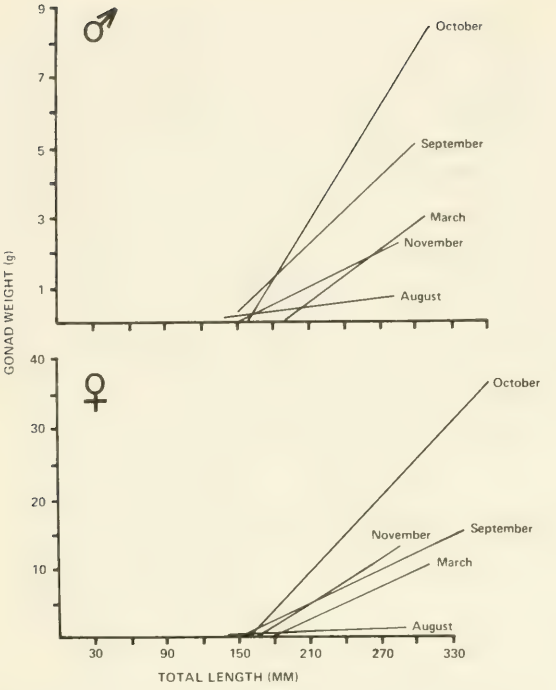

FIGURE 2.—Gonad weight-length regressions for Atlantic croaker by sex and month. The length of each line shows the observed size range.

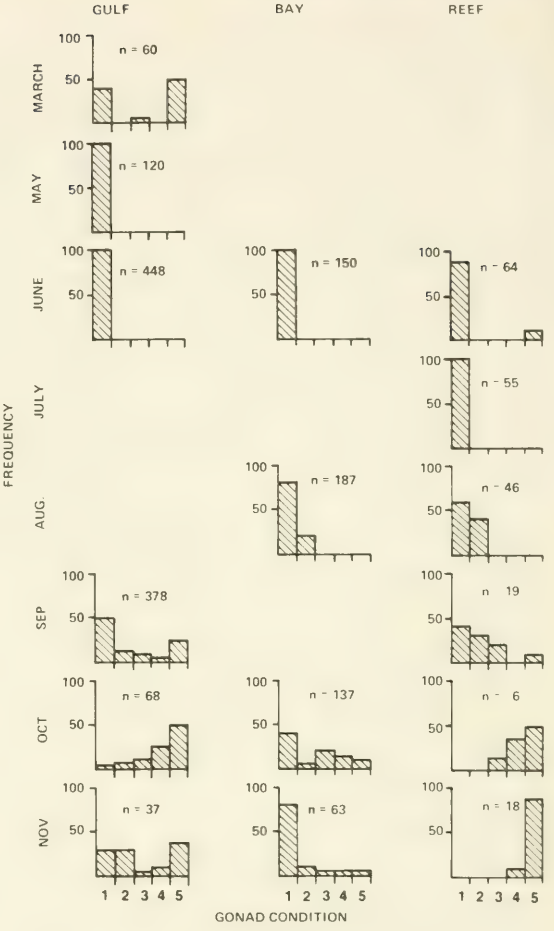

FIGURE 3.—Gonad condition of Atlantic croaker by months and areas. The ordinate represents percent of the sample. Gonad conditions on the abscissa are: (1) immature or resting, (2) maturation, (3) maturity, (4) reproduction, and (5) spent.

(1930), Suttkus (1955), and Bearden (1964); and size at maturity agrees with Pearson (1929), Bearden (1964), Hansen (1969), and Hoese (1973).

The general similarity of croaker reproduction suggests that 15 October, which approximates the time of peak spawning, would be appropriate as a defined hatching date in warm-temperate waters.

SOMATIC WEIGHT VARIATION

Somatic weight-length relationships varied monthly, and these changes appeared to be associated with maturation and spawning. Peak somatic weight occurred during June except in fish smaller than about 140 mm. Somatic weights predicted by the regression equations for other months (Table 2) were compared with predicted weights in June (Figure 4). The somatic weight of individuals smaller than about 140 mm increased from May to at least September. Fish about 140-160 mm showed progressive somatic weight loss from June to September-October. The smallest fish greater than 160 mm, in general, showed the greatest somatic weight loss (or smallest gain); and somatic weight loss, in general, seemed to progressively increase from June to September-October. Somatic weight loss during the fall in fish larger than 140 mm was greatest in September-

TABLE 2.—Analyses for the regressions of somatic weight (Y) in grams on total length (X) in millimeters for each month. All regressions were significant at $\alpha = 0.0001$.

Month	Sample size	r^2	Equation
May	120	0.99	$Y = 39.5303 - 0.8538X + 0.0057X^2$
June	686	0.99	$Y = 71.1692 - 1.3371X + 0.0076X^2$
August	299	0.99	$Y = 120.4035 - 1.9159X + 0.0092X^2$
September	501	0.97	$Y = 158.9511 - 2.3706X + 0.0103X^2$
October	265	0.98	$Y = 148.7089 - 2.2016X + 0.0097X^2$
November	162	0.91	$Y = 73.4739 - 1.2980X + 0.0072X^2$
March	93	0.99	$Y = 132.7087 - 1.8537X + 0.0080X^2$

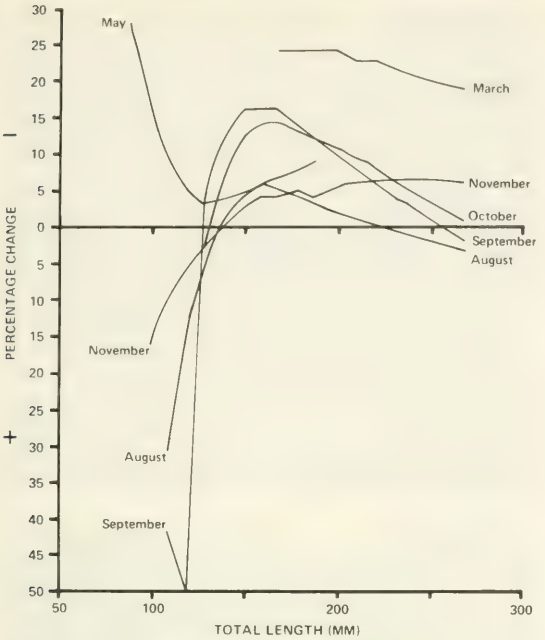

FIGURE 4.—Monthly somatic weight changes in Atlantic croaker. Percentage changes are in comparison to somatic weights in June. The lengths of the curves represent observed size ranges.

October just prior to the time of peak spawning. However, greatest somatic weight loss was observed in March when individuals of 170-250 mm had lost 20-24% of the June weight. The observed somatic weight-length relationships and apparent weight changes in November may be anomalous. Absolute somatic weight decreased in fish smaller than 140 mm, but the percentage weight loss in fish greater than 160 mm was about 5%. Croaker mature at about 140-160 mm, and most fish were small and immature in November. These smaller fish may have just begun to mature for spawning, and their inclusion in the data may have biased the observed pattern in November. This interpretation is supported by the regression coefficients of X and X^2 which were markedly smaller during November than during other months in the August-March period (Table 2).

Somatic weight changes have not been reported for croaker. Additional data, especially from the post-peak spawning period December to February, are needed to fully understand their annual cycle of somatic weight change. Possibly, the percentage of somatic weight loss may be greater in late fall and winter than we observed in March.

AGE DETERMINATION AND GROWTH

General Basis for the Method of Age Determination

Scale marks similar to annuli were distinguished by standard criteria, especially cutting over and differential spacing of circuli. Croaker appear to form two marks on their scales each year except that no mark is formed during their first winter. Some fish form no mark during their first year if 15 October is defined as the hatching date of croaker. Even-numbered marks (cold-period marks) form from about December to March, and odd-numbered marks (warm-period marks) form from about May to November. Fish that do not form a mark in their first year would not have mark numbering that corresponds to the typical odd and even system. Cold-period marks were most distinct and were used as "year" marks, although they represent 1-1½ yr of growth. Recognition of the first cold-period mark is the basis for this method. Subsequent marks, especially cold-period marks, seem to be easily identified.

Age determination was validated by: 1) establishing the time of year when each mark forms, 2) establishing age through analysis of length frequencies, and 3) showing that modes of back-calculated and observed lengths at each age agree with age determination by length frequencies.

Repeated reading suggests this method of age determination is consistent. We found 91% agreement between the first reading of scales from 200 fish (112 age 0 and 88 age I) and a second reading 3 mo later.

We have suggested 15 October as a defined hatching date for croaker. Definition of a hatching date is essential in age and growth studies, so that year classes and age groups can be referenced. In the northern hemisphere 1 January is a standard defined hatching date. That date is convenient and has biological reality, especially for species that spawn in the spring and summer of one year. In more northerly waters, furthermore, growth seasons tend to be short; and spawning tends to be restricted in time and often occurs about when the annulus forms. Croaker of the Carolinian Province, in contrast, have a long, possibly year-round, growing season; and their spawning "season" is so long that it takes place over much of two calendar years. Therefore, it seems more convenient and biologically sound to select their

peak spawning period as a defined hatching date upon which year class and age group terminology is based. Using an October hatching date, the year class would pertain to the fall calendar year and would include any fish of that spawning cycle hatched in the following winter and spring. A virtual annulus would be designated as of October.

Characteristics of Scale Markings Used to Determine Age

The first mark is typically a more or less indistinct mark formed in warm periods. It is characterized by cutting over in the lateral field, but it has little or no differential spacing of circuli before and after the mark (Figure 5a). This mark is often difficult to distinguish after the heavier second mark is formed. The typical second mark is formed in cold periods. It is the most diagnostic feature for age determination in croaker, and its recognition is the basis for our method. This mark is characterized by heavy cutting over of circuli and differential spacing of circuli in the lateral field (Figure 5b). Generally, circuli are closely spaced before the second mark and more widely spaced after it. When the first mark is absent or difficult to see, the typical second mark is readily distinguished. The third mark is typically formed in warm periods and is similar to the first mark (Figure 5c). We examined only six fish whose scales had the fourth mark, and its criteria may need modification. However, the fourth mark apparently forms in cold periods and apparently resembles the second mark in having heavy cutting over and differential spacing of circuli (Figure 5c).

Croaker from a broad geographical range seemingly can be aged by the method proposed, although further work is needed to establish this. Scales of fish from Mississippi, Fort Pierce (Figure 6a), and Chesapeake Bay (Figure 6b, c) showed markings similar to those on scales from Texas fish. Croaker scales from Florida generally had more or less indistinct cutting over and seemed

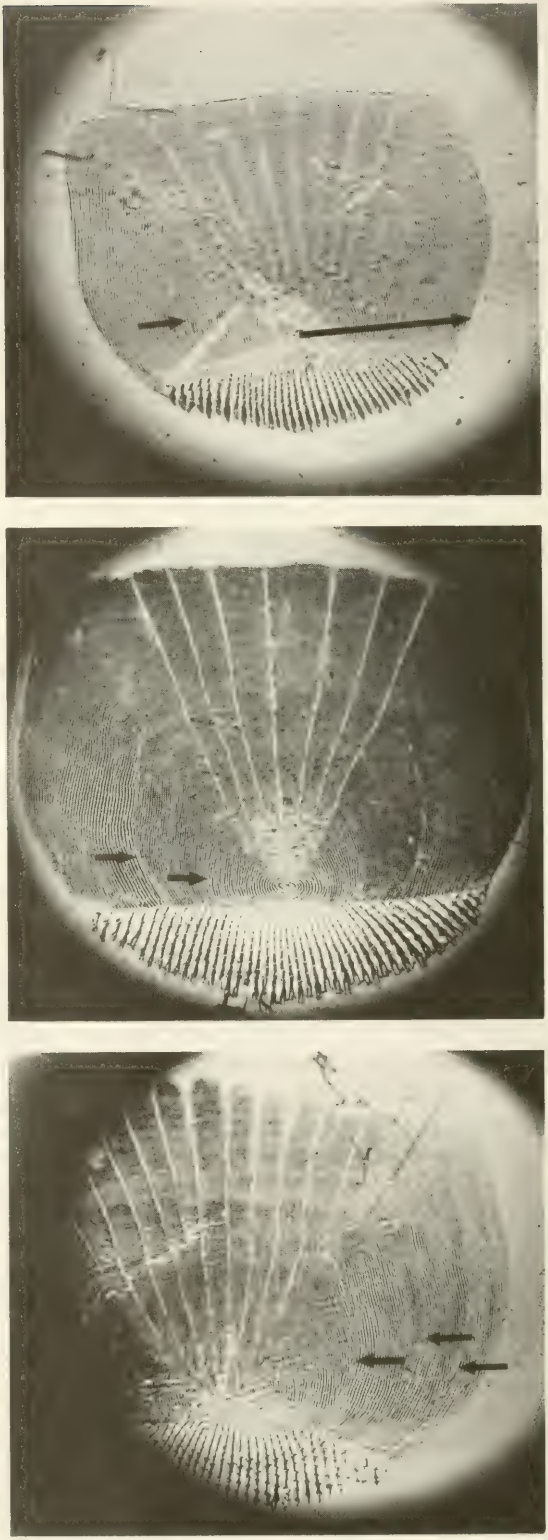

FIGURE 5.—Top. Scale from a 190-mm croaker showing mark 1. This fish was approaching age I when it was captured off Texas in September. The axis depicted shows how measurements were made to determine when each mark formed. Middle. Scale from a 255-mm croaker showing marks 1 and 2. This fish was approaching age II when it was captured off Texas in August. Bottom. Scale from a 310-mm croaker showing marks 2, 3, and 4. This was an age II+ fish captured off Texas in March.

difficult to read, possibly because the fish were collected in tropical waters of southern Florida where temperature changes are not as extreme as further north. Only six fish from Texas had scales with four marks. In contrast, scales from some Chesapeake Bay fish had six marks (Figure 6c). Croaker that live in the Carolinian Province south of Cape Hatteras live only 1 or 2 yr (see General Discussion) and, therefore, tend to have comparatively few marks on their scales. These fish might be easier to age than croaker that live north of Cape Hatteras. The latter fish apparently survive longer and, therefore, probably tend to have more marks on their scales.

Times of Mark Formation

The time when each annuluslike mark formed was determined by plotting for each month the distance from the scale margin to the last mark. Distance was measured across the lateral field of the scale (Figure 5a). Croaker generally form two marks per year except during their first year. Scales with no marks had the smallest distance between the scale margin and focus in May (Figure 7). The radius increased from May to October as scales grew during that period. Therefore, apparently no mark is formed during the first winter; and some croakers form no mark during the first year of life if 15 October is defined as their hatching date. Scales with one mark had the mark closest to the scale edge in warmer months. In March the mark was far removed from the scale margin, suggesting that the first mark normally forms in warm months. Apparently this mark formed on some fish throughout the period May to at least October. The increment between the scale margin and the first (or third) mark did not increase with time, but the reason for this is not clear. Scales with two marks showed the second mark closest to the scale margin in March. The increment between this mark and the scale edge increased until June and then remained nearly constant through November. Therefore, the second mark apparently forms during the colder

FIGURE 6.—Top. Scale from a 305-mm croaker showing marks 1, 2, 3, and 4. This was an age II+ fish when it was captured off Florida in March. Middle. Scale from a 293-mm croaker showing marks 1 and 2. This fish was approaching age II when it was captured in Chesapeake Bay in July. Bottom. Scale from a 508-mm croaker showing marks 1, 2, 3, 4, 5, and 6. This fish was approaching age IV when it was captured in Chesapeake Bay during July.

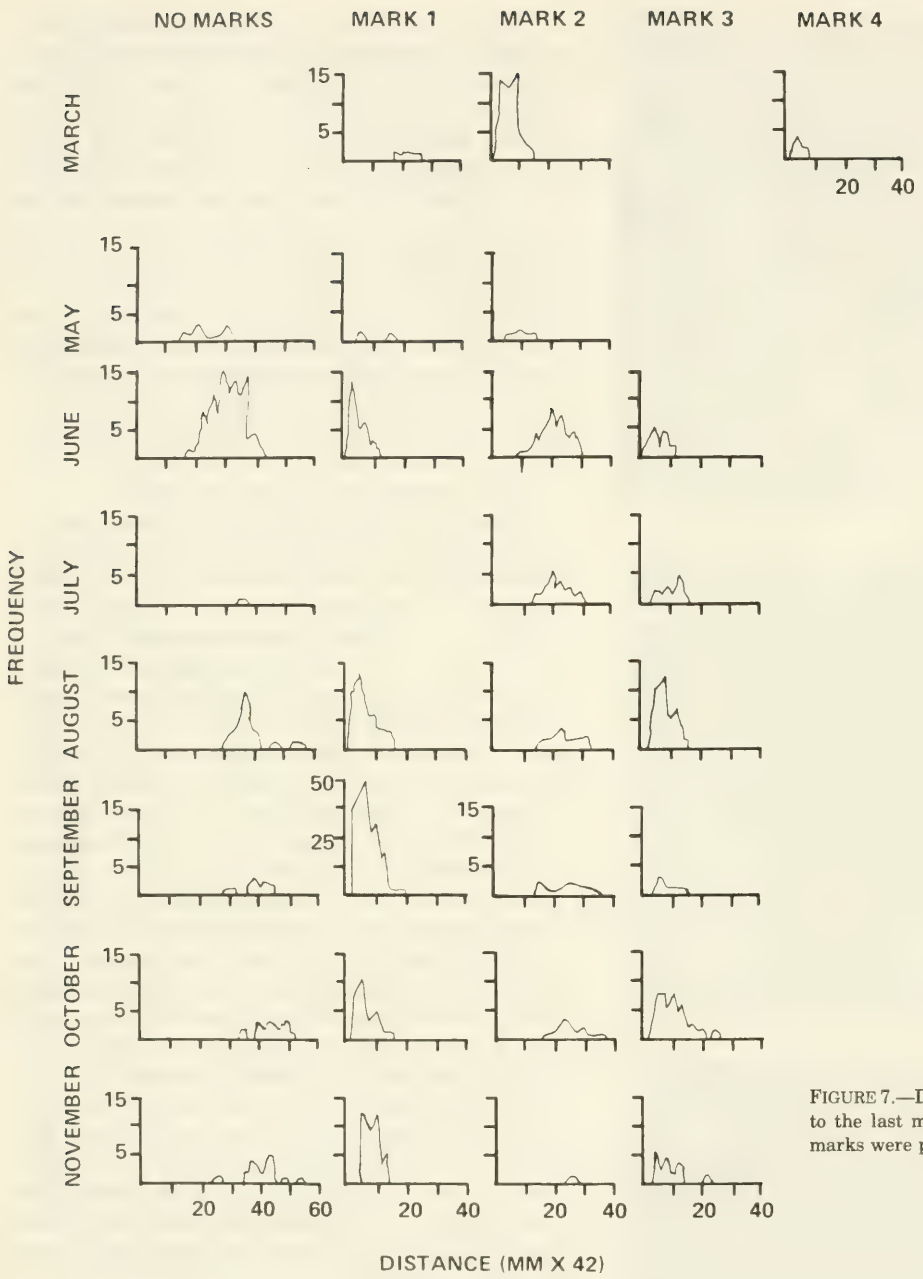

FIGURE 7.—Distance from scale margin to the last mark or to the focus if no marks were present.

months. Scales with three marks showed the third mark being formed throughout the warm months, the only period when scales with only three marks were available. Scales with four marks were observed only during March. The increment on these scales suggests that the fourth mark was formed during winter or spring. However, further data are needed to establish this.

Our findings on times of mark formation agree with Haven's (1954) suggestion that croaker form one fall and one winter mark each year in Chesapeake Bay and with Richards' (1973) computer-simulated findings that the related black drum, *Pogonias cromis,* forms one mark a year until maturity and two marks a year thereafter.

Age Determination and Growth by the Length-Frequency Method

Our length-frequency distributions suggest two croaker year classes occurred off Texas. One age group greatly predominated in the length frequencies of trawl-caught fish from the bay and Gulf during June (Figure 1). The size range of that age group was primarily about 100-150 mm in the bay and about 120-160 mm in the Gulf. Young-of-the-year first appear in Texas bays about November and increase in size from about 10-50 mm during January to 30-85 mm in March, 40-100 mm during May, and 70-130 mm in June (Gunter 1945; Parker 1971; Gallaway and Strawn 1974). Therefore, the fish we captured by trawling during June must be young-of-the-year. These young-of-the-year fish grew to about 110-170 mm in August, 120-175 mm in September, and 140-180 mm in October when they reached age I. Similar sizes in October have been recorded by Gunter (1945), Parker (1971), and Gallaway and Strawn (1974). The fish that became age I in October were about 130-190 mm in November, and fish captured in March were about 165-220 mm. The large fish caught in June by angling near the oyster reef were about 190-270 mm and apparently were survivors of the year class that became age I on the preceding 15 October. These age I+ fish were about 200-310 mm in September when they approached age II. This agrees with Gunter's (1945) size estimates for age II croakers off Texas.

With minor differences, length frequencies reported throughout the Carolinian Province by many workers, including Hildebrand and Cable (1930), Gunter (1945), Suttkus (1955), Bearden (1964), Hansen (1969), Christmas and Waller (1973), Hoese (1973), and Gallaway and Strawn (1974), show growth and age composition similar to our findings. Growth north of Cape Hatteras seems similar to that in the Carolinian Province. Haven (1957) presented monthly length frequencies of fish he considered young-of-the-year. His fish ranged from about 150 to 220 mm in September, but the mode was about 175-180 mm.

Agreement of Observed and Back-Calculated Lengths with Length-Frequencies

Observed sizes at ages 0, I, and II agree closely with ages determined by length frequencies (Figure 8). Only age 0 fish were captured in May and age I fish in July, so that graphs are not presented for these months. The frequencies show overlap in size between the various ages each month. This is to be expected, especially in a species having a prolonged spawning season, and makes it impossible to use the length-frequency method to assign age confidently where sizes at age overlap. The observed lengths of age 0 fish in September were primarily 130-170 mm (mean = 151 mm), but they ranged from about 110 to 220 mm. This age group was about 140-220 mm (mean = 158 mm) during October when they became age I and about 130-220 mm (mean = 172 mm) during November. The observed lengths of age I fish in September were about 200-340 mm with the mean being 253 mm. This age group was about 190-360 mm (mean = 274 mm) in October when they became age II.

Lengths back-calculated to cold-period marks reasonably agree with the sizes at age I estimated by length frequencies in October (Figure 9). However, cold-period marks apparently begin to form generally after October; so that the back-calculated lengths should be larger than the observed lengths in October. The similarity suggests Lee's phenomenon, possibly due to selective mortality favoring survival of smaller croaker. Back-calculated lengths were somewhat smaller than the sizes at age I+ in March, as would be expected. Back-calculated lengths from age I+ fish were primarily 110-210 mm at age I with a mean length of 165 mm. In agreement, back-calculated lengths from six age II+ fish had a mean of 181 mm at age I and 270 mm at age II. The body-scale regression equation used to back-calculate length was:

$$Y = 2.6000 + 4.6389X - 0.0122X^2$$

where Y represents total length in millimeters, and X represents the scale radius (millimeters $\times$ 42). The sample size was 1,123, and the total length range was 90-360 mm. About 88% of the variation in total length was associated with variation in scale radius.

Growth estimates based upon the length-frequency method and from observed and back-calculated estimates using the scale method show very close agreement. Mean lengths in October were about 155-165 mm at age I and 270-280 mm at age II depending upon how age was determined. The wide back-calculated and observed size ranges found at age may be due to the long

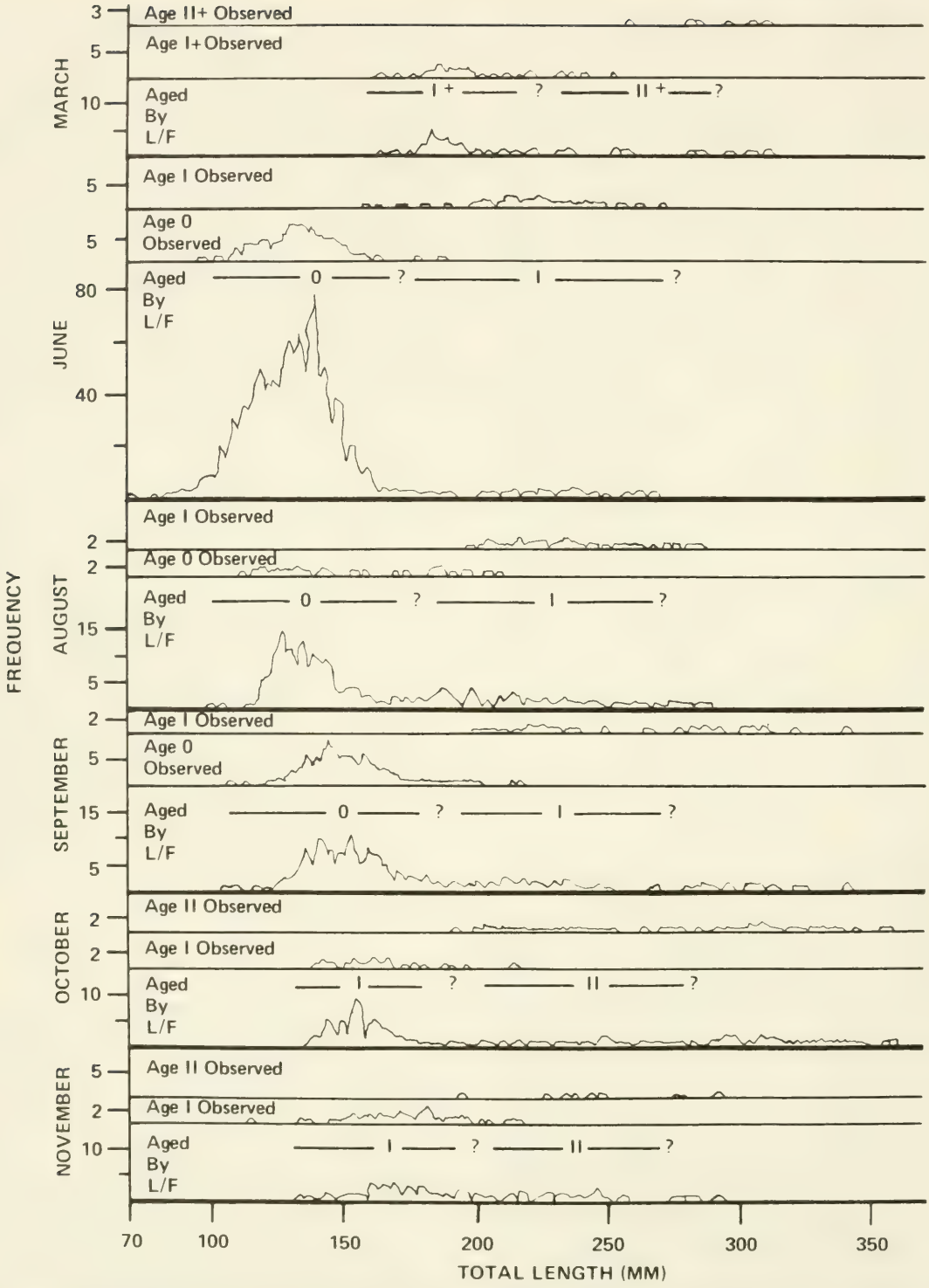

FIGURE 8.—Length compositions comparing observed ages with ages determined by the length-frequency method. Frequencies are moving averages of three.

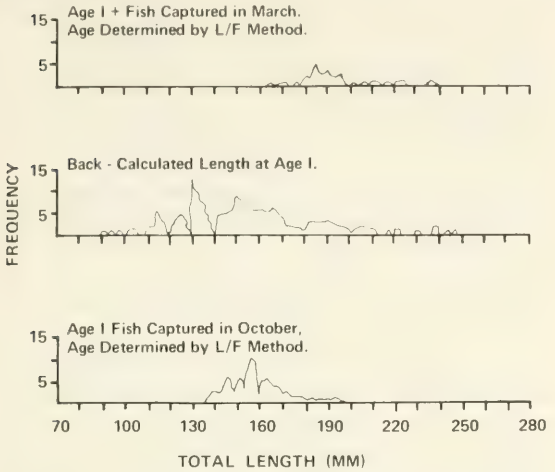

FIGURE 9.—Back-calculated length frequencies at age I and length frequencies (L/F) of age I fish in October and age I+ fish in March. Frequencies are moving averages of three.

spawning season and/or prolonged time span when the cold-period mark may form.

HABITAT SEGREGATION BETWEEN AGE GROUPS

A portion of all croaker age groups apparently utilized bays as feeding grounds during the warmer months, but age I and older fish seemed to occupy different habitat than young-of-the-year. Croaker captured by angling near the oyster reef from June to August were about 200-270 mm in length (Figure 1) and seemed common there. In contrast, trawl-caught bay fish were generally much smaller than 200 mm. Reef and trawl-caught bay individuals were then about age I+ and age 0, respectively. Many other workers, including Reid (1955), Perret (1966), Nelson (1969), Hansen (1969), Parker (1971), Hoese (1973), and Gallaway and Strawn (1974), have also captured few individuals greater than 200 mm by trawling in bays, but they captured many small specimens like we did. Therefore, although capture by angling may have selected larger fish near the reef, the two age-groups seem to segregate by habitat: young-of-the-year occupy soft substrates, and age I and older fish occur near oyster reefs (and similar hard substrates?). This agrees with Harden Jones' (1968) generalization that the feeding grounds of adult fishes are separate from their spawning grounds and nurseries.

Age I and older fish seemed to remain near oyster reefs until they migrated to sea to spawn. Fish caught near oyster reefs were much larger than those caught by trawling in the Gulf or bays until September-October (Figure 1). Specimens larger than 191 mm were not collected in the Gulf until September, which is about when spawning begins in the northern Gulf (Gunter 1945; Suttkus 1955; present study). Simmons and Hoese (1959) captured fish less than 175 mm long throughout the summer as they migrated to the Gulf, but these workers captured fish similar in size to our reef fish only during September.

The larger young-of-the-year began moving to sea by late spring or early summer. Trawl-caught fish in the bay were smaller than those in the Gulf during June (Figure 1) when modal length for young-of-the-year was about 120 mm in the bay and about 140 mm in the Gulf. The difference in size between young-of-the-year in the bay and Gulf agrees with Gunter (1945), Haven (1957), and Reid and Hoese (1958) who found a size gradient in estuaries, the smallest young-of-the-year being farthest up the estuary. Haven (1957) and Hoese et al. (1968) suggested that the gradient was due to gradual seaward dispersal of the largest young, and Parker (1971) and Franks et al. (1972) suggested that young-of-the-year began moving to sea at about 85-100 mm long. Evidently the Gulf becomes a very important nursery by midspring or early summer, because young croaker compose about 24-29% by number of the fishes found on the white shrimp grounds of the Gulf then (Miller 1965, table 3; Chittenden and McEachran 1976).

MAXIMUM SIZE AND AGE, LIFE SPAN, AND MORTALITY RATE

Croaker in the Carolinian Province are typically small and have a short life span and high mortality rate. Most fish we collected were less than 200 mm long and the largest was 357 mm. The largest croaker observed in warm-temperate waters generally have been less than 300 mm (many workers including Hildebrand and Cable 1930; Reid 1955; Bearden 1964; Miller 1965; Nelson 1969; Hansen 1969; Parker 1971; Hoese 1973), although some workers captured fish as large as 330-380 mm (Pearson 1929; Gunter 1945; Suttkus 1955; Franks et al. 1972; Christmas and Waller 1973). Rivas and Roithmayr (1970) found a 668 mm specimen, but this is exceptional.

Our length frequencies suggest that two year classes occurred, but only one was abundant. This agrees with other reported length frequencies from warm-temperate waters (see references cited in section on Age Determination and Growth by the Length-Frequency Method). Therefore, the typical croaker life span in warm-temperate water appears to be only 1 or 2 yr. Age II+ fish captured in March were the oldest fish we examined in agreement with other estimated maximum ages from the Carolinian Province (Gunter 1945; Suttkus 1955; Bearden 1964; Hoese 1973). Fish associated with oyster reefs are larger and a year older than trawl-caught bay or Gulf fish during the summer. However, the abundance of these age I croaker must be small compared with the abundance of age 0 croaker, because the geographical area occupied by oyster reefs is comparatively small.

Croaker have a high total annual mortality rate as their short life span requires. We found only six age II+ fish in 1,123 aged. Greatest mixing of age-groups probably coincides with fall spawning in the Gulf. We observed 11 age I+ and 250 age 0+ fish in random samples from trawl catches made 25-27 September 1974, so that the observed total annual mortality rate was about 96% assuming negative exponential survivorship. This must approximate the total annual mortality rate throughout the Carolinian Province because maximum sizes and ages, length frequencies, and life spans appear similar throughout this area. The observed total annual mortality rate agrees closely with the theoretical total annual mortality rate. Following the reasoning of Royce (1972:238) the negative exponential survivorship relation $S = N_t/N_o = e^{-Zt}$ can be solved for an approximate instantaneous total mortality rate over the entire life span which can be used to estimate average annual total mortality rates. A species with a life span of 1 or 2 yr would have a theoretical approximate total annual mortality rate of 90-100%.

TOTAL WEIGHT-LENGTH AND GIRTH-LENGTH RELATIONSHIPS

The regression of total weight in grams (Y) on total length in millimeters (X) was expressed by the equation:

$$\log_{10} Y = -5.26 + 3.15 \log_{10} X.$$

This relationship was based on a sample size of 2,081 fish in the length range 90-360 mm. About 98% of the variation in $\log_{10}$ total weight was associated with variation in $\log_{10}$ total length. The arithmetic mean $\log_{10} X$ was 2.21056, and arithmetic mean $\log_{10} Y$ was 1.71546.

The regression of girth in millimeters (Y) on total length (X) in millimeters was expressed by the linear equation:

$$Y = -11.84 + 0.71X.$$

This relationship was based on a sample size of 2,081 fish in the length range 90-360 mm. The arithmetic mean girth was 108.07 mm. About 94% of the variation in girth was associated with variation in total length.

GENERAL DISCUSSION

Many aspects of the life history of Atlantic croaker in the Carolinian Province appear different than those of fish found in cold-temperate waters north of Cape Hatteras except that the growth rates appear similar. In general, our data and the literature agree that in warm-temperate waters: 1) peak spawning occurs about October but the spawning season is long and lasts from about September to at least March, 2) maturity is reached at about 140-180 mm long as the fish approach age I, 3) maximum size is about 300-350 mm and most fish are so small (about 200 mm or less in length) that they do not support commercial food fisheries, 4) the life span is about 1-2 yr and maximum age is typically about 2 yr, 5) most fish live only to about age I, and 6) total annual mortality rate is about 95%. In contrast, fish living north of Cape Hatteras generally:

1) Have a spawning season (July or August-December?) that starts earlier and may end earlier (Welsh and Breder 1924; Hildebrand and Schroeder 1928; Wallace 1940; Pearson 1941; Massmann and Pacheco 1960). However, the time when spawning ends is not certain. Haven (1957) captured many young 20-30 mm TL from February to April, but their significance is not clear; they could represent late-winter spawning or, perhaps, fall spawning with little or no overwinter growth. Peak spawning seemingly occurs no later than midfall, because all the adult fish that Wallace (1940) examined had spent or

recovering gonads in late November and thereafter.

2) Reach maturity when greater than 200 mm long as they approach at least age II (Welsh and Breder 1924; Wallace 1940; Haven 1954).
3) Have a maximum size of about 500 mm (Hildebrand and Schroeder 1928; Gunter 1950) and large average size so that they have supported important commercial food fisheries (Gunter 1950; Haven 1957; Joseph 1972).

Maturity is reached about 1 yr later in cold-temperate waters and typical sizes are much larger, although growth rates appear similar. Therefore, the typical maximum age is probably about 2-4 yr north of Cape Hatteras. If so, the total annual mortality rate must be lower north of Cape Hatteras. Assuming negative exponential survivorship, the theoretical approximate total annual mortality rates would be 90, 78, and 68% for life spans of 2, 3, and 4 yr, respectively.

The existence of an abrupt change at Cape Hatteras in the life histories and population dynamics of species whose ranges traverse this area has apparently not been recognized, particularly as a possible general phenomenon; although Cape Hatteras has long been recognized as a significant zoogeographic boundary [see Briggs' (1974) review]. Gunter (1950) noted differences in the sizes and some aspects of the life histories of certain fishes of the Gulf of Mexico and mid-Atlantic coast of the United States. However, he gave no consideration to the possibility that an abrupt change might occur near Cape Hatteras. Although the Cape Hatteras connection has not been recognized, the pelagic, anadromous American shad, *Alosa sapidissima,* also shows changes in life history there that are similar to those herein documented for croaker. Runs of shad native to streams north of Cape Hatteras consist primarily of somewhat older fish (ages IV-VII and older) and include many repeater spawners in contrast to the younger fish (ages IV-VI) and the complete or virtual absence of repeat spawners south of Cape Hatteras (for pertinent literature see Walburg and Nichols 1967; Chittenden 1975). La Pointe (1958) reported similar growth rates in shad native to streams throughout their range. Therefore, the geographic differences in age compositions should result in differences in life spans, ages at maturity, maximum ages, maximum and average sizes, and mortality rates as in croaker.

The life histories and population dynamics of two species with different life styles but primarily coastal habit have been shown to change abruptly at Cape Hatteras. This may represent a general phenomenon as Gunter (1950) apparently observed. However, similar comparisons are necessary in other species, especially noncoastal forms, to see how far the inference extends.

The reason for the geographical differences in population dynamics is not clear. However, shad exhibit great somatic weight loss (about 25-55% depending upon sex and size) associated with migration and spawning (Leggett 1972; Chittenden 1976). Leggett (1972) suggested that the low frequency of repeat spawning shad in southern streams might be due to increased use of body reserves during spawning migrations that occur at higher average temperatures. Croaker also show somatic weight loss associated with maturation and spawning, although we did not observe weight loss comparable to that in shad. However, we had no data for the post-peak spawning period December-February when weight loss may have been greater. It is pertinent here that Chittenden has observed many emaciated spot, *Leiostomus xanthurus,* in the Gulf of Mexico during January, which is about when this species spawns. The observed differences in population dynamics north and south of Cape Hatteras may be largely the result of different temperature regimes that affect age at maturation, spawning-associated somatic weight loss, and the magnitude of a subsequent post-spawning mortality.

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COASTAL AND OCEANIC FISH LARVAE IN AN AREA OF UPWELLING OFF YAQUINA BAY, OREGON

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ABSTRACT

A 1½-yr survey of planktonic fish larvae collected from 2 to 111 km off the mid-Oregon coast in 1971-72 yielded 287 samples which contained 23,578 individuals in 90 taxonomic groups, 78 identified at the species level.

Two distinct faunal assemblages were found: a "coastal" assemblage 2 to 28 km offshore and an "offshore" assemblage 37 to 111 km from shore. The coastal group was dominated by Osmeridae, *Parophrys vetulus, Isopsetta isolepis,* and *Microgadus proximus*. The offshore group was dominated by *Sebastes* spp., *Stenobrachius leucopsarus, Tarletonbeania crenularis, Lyopsetta exilis,* and *Engraulis mordax*. Peak abundance in both assemblages occurred between February and July when >90% of all larvae were taken. Larval distribution patterns in each assemblage were similar in 1971 and 1972, but larval abundance was greater in 1971 than 1972.

Ninety-nine percent of the larvae in 53 taxa designated as coastal and 96% of the larvae in 31 taxa designated as offshore were taken 2 to 28 km or 37 to 111 km offshore respectively. This separation of coastal and offshore larvae may be explained, in part, by adult spawning locations and current circulation patterns.

The species of larvae present in the coastal assemblage were similar to those in Yaquina Bay, but dominant species were quite different. The coastal zone is an important spawning area for *P. vetulus,* which utilizes Yaquina Bay estuary as a nursery during part of its early life.

In this paper, distribution patterns, seasonality, species composition, dominance, and relative abundance of larval fishes in an upwelling area off Yaquina Bay, Oreg., are described. Included are the most comprehensive time series of data yet available on larval fishes in the northeast Pacific Ocean north of California, data on the greatest number of distinct larval taxa yet reported for this area, and the first quantitative information on coastal and offshore assemblages of larval fishes off the northwest coast of the United States.

Larval fish distributions are discussed in relation to current circulation patterns and spawning location of adults. Results are compared with Pearcy and Myers' (1974) study of larval fishes of Yaquina Bay. The data on fish larvae are compared with data on zooplankton (Peterson and Miller 1975, footnote 2), shrimp larvae (Rothlisberg 1975), and crab larvae (Lough 1975) collected at the same time and location. Distribution patterns of larval fishes off the mid-Oregon coast are discussed in relation to a broader geographic area in the northeast Pacific.

PREVIOUS STUDIES IN THE NORTHEAST PACIFIC

This review includes only studies of a general survey nature conducted in ocean waters from northern California to the Gulf of Alaska, excluding the Aleutian Chain and Bering Sea. Studies in sounds, bays, and estuaries are not considered.

Prior to 1972, data on ichthyoplankton in the northeast Pacific were sparse and essentially nonquantitative because of the gear used—Isaacs-Kidd Midwater Trawls and Northern Pacific area (NORPAC) nets (Motoda et al. 1957). Surveys were designed primarily for biomass estimates of pelagic invertebrates and fishes. The ancillary data on fish larvae, often not identified to species, were usually presented in the form of appendix tables [Aron[3] for northern Washington

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[2]Peterson, W. T., and C. B. Miller. 1976. Zooplankton along the continental shelf off Newport, Oreg., 1969-72: distribution, abundance, seasonal cycle and year to year variations. Oreg. State Univ. Sea Grant Coll. Prog. Publ. ORESU-T-76-002, 111 p.

[3]Aron, W. 1958. Preliminary report of midwater trawling studies in the Pacific Ocean. Univ. Wash. Dep. Oceanogr. Tech. Rep. 58, 64 p.

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to southwest Alaska; Aron[4] for southern California to southwest Alaska; Pearcy[5] for Oregon; Porter (1964) for northern California (flatfish only); LeBrasseur[6,7] for the northeast Pacific; Day (1971) for Washington to British Columbia]. Two additional reports (Aron 1959; LeBrasseur[8]) briefly mentioned larval fishes in the text.

More recent reports have been based on surveys designed specifically to sample ichthyoplankton using meter nets and bongo nets [Waldron (1972) off Oregon, Washington, and British Columbia in April-May 1967; Richardson (1973) off Oregon from May to October 1969; Naplin et al.[9] off Washington and British Columbia in October-November 1971; Dunn and Naplin[10] off Alaska in April-May 1972; Pearcy and Myers (1974) off Yaquina Bay from June 1969 to June 1970]. Results were quantitative and more refined species lists were provided. However most of these studies were restricted in seasonal coverage to periods of less than 1 yr. Pearcy and Myers (1974) presented a year-long data set but listed only yearly mean abundances. Discussion of larval distribution patterns in all these papers was limited. Waldron (1972) arbitrarily divided his data into two groups located inshore or offshore of the 914-m contour and discussed larval abundances in each region. Pearcy and Myers (1974) discussed horizontal variations in larval distributions with respect to larvae that occurred offshore and those that occurred in Yaquina Bay. Vertical distribution and day-night differences have not been discussed, although Richardson (1973) compared deep (to 200 m) and shallow (upper 20 m) tows.

[4]Aron, W. 1960. The distribution of animals in the eastern north Pacific and its relationship to physical and chemical conditions. Univ. Wash. Dep. Oceanogr. Tech. Rep. 63, Ref. 60-55, 65 p. + 156 append.

[5]Pearcy, W. G. 1962. Species composition and distribution of marine nekton in the Pacific Ocean off Oregon. Oreg. State Univ., Dep. Oceanogr., A.E.C. Prog. Rep. 1, Ref. 62-8, 14 p.

[6]LeBrasseur, R. J. 1964. Data record: a preliminary checklist of some marine plankton from the northeastern Pacific Ocean. Fish. Res. Board Can., Manuscr. Rep. Ser. (Oceanogr. Limnol.) 174, 14 p.

[7]LeBrasseur, R. 1970. Larval fish species collected in zooplankton samples from the northeastern Pacific Ocean 1956-1959. Fish. Res. Board Can. Tech. Rep. 175, 47 p.

[8]LeBrasseur, R. J. 1965. Seasonal and annual variations of net zooplankton at Ocean Station P, 1956-1964. Fish. Res. Board Can., Manuscr. Rep. Ser. (Oceanogr. Limnol.) 202, 162 p.

[9]Naplin, N.A., J. R. Dunn, and K. Niggol. 1973. Fish eggs, larvae and juveniles collected from the northeast Pacific Ocean, October-November 1971. NOAA-NMFS Northwest Fish. Cent., MARMAP Surv. I, Rep. 10, 39 p. + 121 tables.

[10]Dunn, J. R., and N. A. Naplin. 1974. Fish eggs and larvae collected from waters adjacent to Kodiak Island, Alaska, during April and May 1972. NOAA-NMFS, Northwest Fish. Cent., MARMAP Surv. I, Rep. 12, 61 p.

MATERIALS AND METHODS

Most data came from samples taken at 12 stations, located 2 to 111 km offshore along an east-west transect (lat. 44°39.1′N) off Newport, Oreg., just north of Yaquina Bay (Figure 1). The transect extended over the continental shelf and slope; depths ranged from 20 to 2,850 m. Samples were taken every month from January 1971 to August 1972 except in January and February 1972, although not every station was sampled

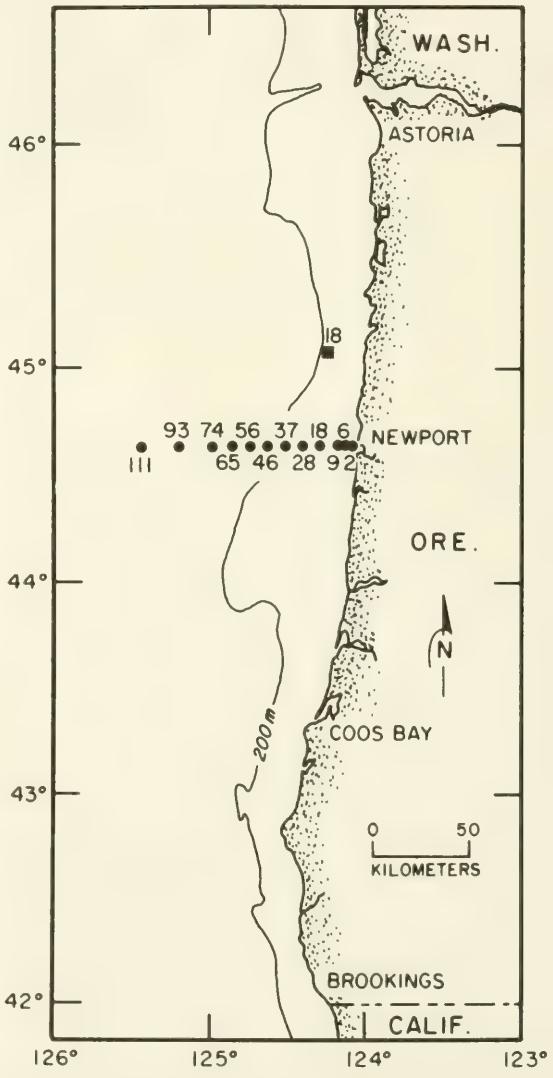

FIGURE 1.—Location of the major bongo net sampling stations (circles) along an east-west transect (lat. 44°39.1′N) off Yaquina Bay, Oreg., and a 24-h station (square) occupied in May 1972. Numbers are kilometers from the coast.

every month (Table 1). Of the 287 station occupancies, 219 were made during daylight, 50 at night, and 18 at dusk or dawn. In addition, a series of replicate tows was made on 28-30 June 1971, which included two daytime and two nighttime hauls at stations 2, 6, and 9 and one daytime and one nighttime haul at stations 46, 56, 65, and 74.

Samples were collected with a 70-cm (mouth diameter) bongo net without a closing mechanism. The bongos had two cylindrical-conical nets of 0.571-mm mesh Nitex[11] which were 4.6 m long and had a filtering area to mouth area ratio of about 10:1. Tsurumi-Seiki Kosakusho (TSK) flowmeters were positioned off center in the mouth of each net. A 40-kg multiplane kite-otter depressor (Colton 1959) was attached to the cable beneath the bongos which produced a 2:1 wire out to depth fished ratio. A time-depth recorder (bathykymograph) was attached to the cable above the bongos to record depth and path of tow.

The net was towed along depth contours parallel to the coast at a vessel speed of 2-3 knots. Tows were made obliquely through the water column in equal stepped intervals from the bottom or 150 m to the surface. Tow times ranged from 8 to 39 min and were usually between 10 and 30 min. Volume of water filtered ranged from 283 to 1,411 m^3 and was usually between 500 and 1,000 m^3.

At each station a bathythermograph (BT) cast was made to the bottom or 140 m, a surface bucket temperature was recorded, and surface and deep (bottom or 140 m) salinity samples were taken.

Plankton samples were preserved at sea in 10% buffered Formalin. One sample from each bongo pair (287 samples) was sorted for fish larvae except for the replicate series where both samples of each pair (7 of the 287 samples plus 33 additional samples) were sorted. All fish larvae were removed from each sample and were stored in 5% buffered Formalin. Larvae were identified to the lowest possible taxonomic group, enumerated, and measured (standard length). Numbers of larvae from each sample were standardized to number under 10 m^2 of sea surface. This standardized number was used in all analyses unless indicated otherwise.

In addition to the above samples, a 24-h station was occupied 18 km offshore at a location 46 km north of the Newport transect at lat. 45°04.0′N (Figure 1) on 30-31 May 1972. Water depth ranged from 158 to 164 m. Four depth strata (0-10, 11-50, 51-100, and 101-150 m) were sampled. Tows were designed to filter approximately the same volume of water in each stratum ($\bar{x}$ = 912 m^3 ± 142). The nonclosing bongo gear was lowered rapidly to the maximum depth of the zone to be sampled, towed obliquely through the depth zone in equally spaced steps, and then retrieved quickly to minimize contamination. Two tows were made in each depth stratum in daylight and again at night, which yielded 32 (16 pairs) samples. All fish larvae were sorted, identified, and enumerated. Numbers

[11]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Summary of 287 station occupancies made on an east-west transect (lat. 44°39.1′N) off Yaquina Bay, Oreg., 1971-72.

	Station (km from coast)											
	2	6	9	18	28	37	46	56	65	74	93	111
	Bottom depth (m)											
Month	20	46	59	85	95	142	330	220	340	1,060	1,300	2,850
1971:												
Jan.	2	2	2	2	—	—	—	—	—	—	—	—
Feb.	2	2	2	2	—	2	—	2	—	1	1	1
Mar.	2	2	2	2	1	2	—	2	1	2	2	2
Apr.	—	—	1	1	1	1	1	1	—	1	1	—
May	3	3	3	3	3	3	3	3	2	2	2	2
June	2	2	2	2	2	2	2	2	2	2	2	2
July	2	2	2	2	1	1	1	1	1	1	1	1
Aug.	2	2	2	2	2	2	2	2	2	2	2	1
Sept.	1	1	1	1	1	1	1	1	1	1	1	1
Oct.	1	1	1	1	1	1	1	1	1	1	1	1
Nov.	1	1	1	1	1	1	1	1	1	1	1	1
Dec.	1	1	1	1	1	1	1	1	1	1	—	—
1972:												
Jan.	—	—	—	—	—	—	—	—	—	—	—	—
Feb.	—	—	—	—	—	—	—	—	—	—	—	—
Mar.	3	2	3	3	3	3	3	3	2	2	2	2
Apr.	2	1	2	2	1	1	1	1	—	—	—	—
May	1	1	1	1	1	1	1	1	1	1	1	1
June	2	2	2	2	2	2	2	2	2	2	2	2
July	1	1	1	1	1	1	1	1	1	1	1	1
Aug.	1	1	1	1	1	—	—	—	—	—	—	—

of larvae from each of these samples were standardized to numbers per 1,000 m^3 of water filtered.

TAXONOMIC PROBLEMS

The 287 samples yielded 23,578 fish larvae in 27 families and 1 order (Table 2). To date 90 taxonomic groups have been identified, 78 at the species level, although 17 of these, primarily in the Cottidae and Stichaeidae, are still only numbered "larval types"[12] which are considered to be identified at the level of distinct species. These larval types have not yet been named because large specimens needed for positive identification were absent from the collections. This is the greatest number of species recorded from a larval fish study in the northeast Pacific which reflects, in part, refinements in larval fish identification as well as the intensity of the sampling effort which yielded many complete developmental series. Many of these larvae, particularly the coastal forms, have not yet been described in detail in the literature.

While identification of many of the abundant larvae, particularly the pleuronectids and myctophids, has been accomplished with certainty, a few major taxonomic problems remain, most notably with the osmerids and the scorpaenids, primarily *Sebastes* spp. We have not yet been able to identify the larval osmerids (<30 mm) to species, of which there are five possibilities: *Allosmerus elongatus, Hypomesus pretiosus, Spirinchus starksi, Spirinchus thaleichthys,* and *Thaleichthys pacificus.* Available descriptions (Morris[13]; Yap-Chiongco 1941; DeLacy and Batts[14]; Dryfoos 1965; Moulton 1970) are inadequate to distinguish all five species. We have not even established "larval types" below the family level.

No attempt was made to separate *Sebastes* spp., another problem group, into "larval types" (species or species groups) although a few distinct kinds appeared to be present. Samples from Oregon waters may contain some 35 species and identification of the larvae is difficult (Moser 1967, 1972; Moser et al. in press).

One other problem group is the Cyclopteridae. Based on its broad distribution pattern, our Cyclopteridae spp. 1 probably represents a multispecies group, perhaps *Liparis* spp., but we have not yet been able to subdivide it on the basis of larval characters.

These identification problems impose limitations on analysis of ichthyoplankton data. Caution must be exercised in interpretation of results when multispecies groups constitute a major proportion of larvae taken, such as *Sebastes* spp. and osmerids off Oregon.

SAMPLING VARIABILITY

A series of replicate oblique tows (four day and four night samples at stations 2, 6, 9; two day and two night samples at stations 46, 56, 65, 74) made in June 1971 was examined to assess sampling variability. Species composition of day and night tows at a station was similar, based on common larvae collected and their relative rank abundance. Total larvae in night catches exceeded those in day catches at all stations except 65 and 74 (Figure 2). Large day-night differences occurred at stations 6 and 9. This was primarily due to increased catches of large (>23 mm) osmerid larvae at night (Figure 3), which presumably avoided the net by day or were deeper, although 76 to 87% of the water column was sampled in daytime. Even so, osmerids were the most abundant larvae captured in all samples from these two stations. At station 2, the increased night catches were due to an increase in the numbers of large larvae (including osmerids), as well as an increase in the number of species captured (7-10 in daytime vs. 13-14 at night). Both *Isopsetta isolepsis* (most >16.5 mm) and *Microgadus proximus* (most >29 mm), species common at stations 6 and 9 during day and night, were collected only at night at station 2. At stations 46 and 56, night catches yielded increased numbers of *Engraulis mordax* (4-10 mm) and *Stenobrachius leucopsarus* (4-15 mm) while night catches of *Sebastes* spp. (3-9 mm) were half the daytime numbers (3-12 mm). At station 65, *E. mordax* (6-10 mm) was again more abundant in night tows while *Stenobrachius leucopsarus* was much less abundant at night, composing only 10 and 34% of the numbers of larvae in the two nighttime tows (6-13 mm) but 61 and 54% in the two

[12]The term larval type used in this paper refers to a particular kind of larva which may be distinguished from other larvae on the basis of larval characters but which has not yet been named. The term does not necessarily denote identification to the species level and is not intended to have any taxonomic implications.

[13]Morris, R. Some notes on the early life history of the night surf smelt, *Spirinchus starski* (Fisk) 1913. Unpubl. manuscr., 37 p.

[14]DeLacy, A. C., and B. S. Batts. 1963. A search for racial characteristics in the Columbia River smelt. Res. Fish., Fish. Res. Inst. Univ. Wash. Contrib. 147:30-32.

TABLE 2.—Species composition[1] and abundance[2] of fish larvae taken 2 to 111 km off of Yaquina Bay, Oreg., from January 1971 to August 1972.

Taxa	Total standardized abundance[2] Coastal	Offshore
Clupeidae:		
+ *Clupea harengus pallasi* (c)	64.19	0
Engraulidae:		
+– *Engraulis mordax* (o)	13.39	1,000.70
Osmeridae:		
+– Undetermined spp. (c)	5,749.53	13.65
Bathylagidae:		
– *Bathylagus milleri* (o)	0	2.90
– *Bathylagus ochotensis* (o)	0	131.46
– *Bathylagus pacificus* (o)	0	34.18
Melanostomiatidae:		
– *Tactostoma macropus* (o)	0	2.05
Chauliodontidae:		
– *Chaulidous macouni* (o)	0	29.47
Paralepididae:		
– *Lestidiops ringens* (o)	0	5.78
Myctophidae:		
+– *Lampanyctus regalis* (o)	0.82	37.04
– ?*Loweina rara*[3] (o)	0	1.15
– *Protomyctophum crockeri* (o)	0	34.03
+– *Protomyctophum thompsoni* (o)	9.97	173.77
+– *Stenobrachius leucopsarus* (o)	45.30	3,648.00
+– *Tarletonbeania crenularis* (o)	2.29	635.20
– Undetermined spp. (o)	0	7.24
Gadidae:		
+– *Microgadus proximus* (c)	580.28	5.44
Ophidiidae:		
– *Brosmophycis marginata* (o)	0	2.86
– Ophidiidae sp. 1 (o)	0	1.32
Scorpaenidae:		
+– *Sebastes* spp. (o)	180.66	3,967.82
+– *Sebastolobus* spp. (o)	0.60	19.21
Hexagrammidae:		
+– *Hexagrammos* spp. (o)	0.44	2.94
+– *Ophiodon elongatus* (c)	53.44	1.24
Anoplopomatidae:		
+– *Anoplopoma fimbria* (o)	0.93	7.34
Cottidae:		
+– *Artedius* sp. 1 (c)	189.26	7.94
+ *Artedius* sp. 2 (c)	139.96	0
+ *Chitonotus pugetensis* (c)	7.55	0
+ *Cottus asper* (c)	145.43	0
+– *Enophrys bison* (c)	60.65	6.63
+– *Hemilepidotus hemilepidotus* (c-o)	13.13	6.44
+– *Hemilepidotus spinosus* (c-o)	69.04	29.78
+– *Icelinus* sp. 1 (c)	54.46	1.94
+– *Leptocottus armatus* (c-o)	18.60	5.50
+ *Nautichthys oculofasciatus* (c)	0.77	0
+ *Oligocottus* sp. 1 (c)	3.15	0
+ *Paricelinus hopliticus* (c)	0.79	0
– *Psychrolutes*-like sp. 1 (o)	0	2.21
+– *Radulinus asprellus* (c)	58.45	9.19
+ *Rhamphocottus richardsoni* (c)	0.77	0
+ *Scorpaenichthys marmoratus* (c)	21.84	0
+ Cottidae sp. 1C (c)	5.94	0
+ Cottidae sp. 12 (c)	42.70	0
+ Cottidae sp. 19 (c)	0.33	0
+ Cottidae sp. 20 (c)	1.12	0
+ Undetermined spp. (c)	21.55	0
Agonidae:		
+ *Agonopsis emmelane* (c)	1.17	0
+– *Bathyagonus* spp. (c-o)	1.55	1.75
+ *Occella verrucosa* (c)	13.27	0
+ *Odontopyxis trispinosa* (c)	1.48	0
+ *Pallasina barbata* (c)	0.87	0
+ *Stellerina xyosterna* (c)	28.43	0
+ *Zeneretmus latifrons* (c)	1.16	0
+ Agonidae sp. 6 (c)	3.14	0
Cyclopteridae:		
+ *Liparis pulchellus* (c)	15.85	0
+– Cyclopteridae spp. 1 (c-o)	34.09	79.70
+ Cyclopteridae sp. 3 (c)	4.45	0
+– Undetermined spp. (c)	27.04	6.75
Bathymasteridae:		
+– *Ronquilus jordani* (c)	32.47	3.35
Blennioids:		
+ Undetermined spp. (c)	0.32	0
Clinidae:		
+ *Gibbonsia ?montereyensis* (c)	0.70	0
Stichaeidae:		
+ *Anoplarchus* sp. 1 (c)	33.81	0
+ *Chirolophis* sp. 1 (c)	37.80	0
+ *Lyconectes aleutensis* (c)	1.03	0
+ *Lumpenus sagitta* (c)	1.37	0
+ *Plectobranchus evides* (c)	1.12	0
+ Stichaeidae sp. 1 (c)	0.77	0
+– Stichaeidae sp. 2 (c)	5.53	1.04
+ Stichaeidae sp. 4 (c)	6.56	0
Ptilichthyidae:		
+ *Ptilichthys goodei* (c)	1.09	0
Pholidae:		
+ *Apodichthys flavidus* (c)	0.70	0
+ *Pholis* spp. (c)	71.17	0
Icosteidae:		
– *Icosteus aenigmaticus* (o)	0	15.60
Ammodytidae:		
+ *Ammodytes hexapterus* (c)	258.50	0
Gobiidae:		
+ *Clevelandia ios* (c)	2.31	0
Centrolophidae:		
– *Ichichthys lockingtoni* (o)	0	60.30
Bothidae:		
– *Citharichthys sordidus* (o)	0	1.80
+ *Citharichthys stigmaeus* (c)	2.59	0
+– *Citharichthys* spp.[4] (o)	7.53	57.19
Pleuronectidae:		
– *Atheresthes stomias* (o)	0	4.80
+– *Embassichthys bathybius* (o)	0.64	7.09
– *Eopsetta jordani* (o)	0	1.57
+– *Glyptocephalus zachirus* (o)	18.27	113.81
+– *Hippoglossoides elassodon* (c-o)	2.70	2.59
+– *Isopsetta isolepis* (c)	1,157.90	12.53
+– *Lepidopsetta bilineata* (c)	1.31	0
+– *Lyopsetta exilis* (o)	96.54	475.23
+– *Microstomus pacificus* (o)	8.24	81.74
+– *Parophrys vetulus* (c)	1,479.59	37.62
+– *Platichthys stellatus* (c)	187.40	1.72
+– *Psettichthys melanostictus* (c)	308.12	1.13
Unidentified larvae	16.84	17.22
Fragments	47.71	49.09
	11,474.46	10,868.04

[1]General distribution patterns are given for each taxon:
+ = taken 2 to 28 km offshore
– = taken 37 to 111 km offshore
c = coastal type (>80% of all larvae taken 2 to 28 km from coast)
o = offshore type (>80% of all larvae taken 37 to 111 km from coast)
c-o = neither c or o type (<80% of all larvae taken in either coastal or offshore area).

[2]The sum of the standardized numbers (number under 10 m^2 sea surface) of larvae from each sample in the coastal (2-28 km) and offshore (37-111) km assemblages (139 and 148 samples, respectively).

[3]Identification based on one partly mutilated specimen.

[4]Specimens too small to identify to species.

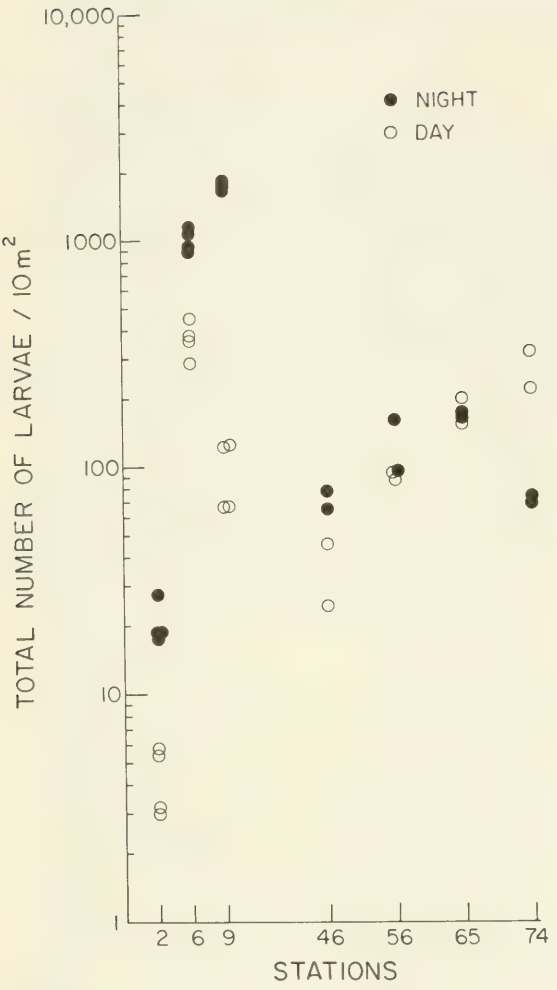

FIGURE 2.—Day and night catches of fish larvae on transect off Yaquina Bay, Oreg., June 1971.

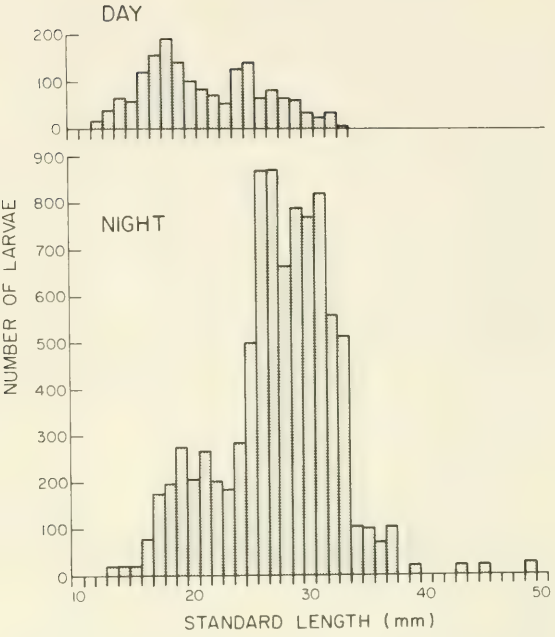

FIGURE 3.—Day and night length frequencies of osmerid larvae collected at 6 and 9 km off Yaquina Bay, Oreg., June 1971. Numbers of larvae were combined for both nets from four day and four night hauls.

daytime tows (4-16 mm). Decreased larval abundances at night at station 74 were due mainly to reduced numbers of *S. leucopsarus* (5-13 mm at night, 5-16 mm in day). Thus avoidance of the net by large larvae in daytime seemed to account for much of the day-night variation at the coastal stations 2, 6, and 9. Differences at the offshore stations may have been due to patchiness of small larvae.

Variability among repeated samples was examined at the three inshore stations where four day and four night replicate samples were taken at each station. Coefficients of dispersion were calculated for total larvae, osmerids, and total larvae minus osmerids (Table 3). Values were close to 1.0 for total larvae minus osmerids at stations 6 and 9 and for total larvae at station 2 where osmerids were not abundant suggesting that larvae were randomly distributed. Coefficients were large, however, for total larvae and for osmerids at 6 and 9 where smelt larvae were abundant, except at night at station 9. These large coefficients of dispersion indicate high contagion, possibly caused by schooling behavior of large osmerid larvae.

TABLE 3.—Coefficients of dispersion ($s^2/\bar{x}$) for total larvae, osmerids, and total larvae minus osmerids in replicate tow series made in June 1971 on the transect (lat. 44°39.1′N) off Yaquina Bay, Oreg.

Item	Station 2		Station 6		Station 9	
	Day	Night	Day	Night	Day	Night
Total larvae	0.49	0.97	12.44	11.96	11.56	0.57
Osmeridae			16.40	12.81	14.49	0.82
Total larvae minus Osmeridae			0.81	3.18	0.81	1.23

VERTICAL DISTRIBUTION

One attempt was made to study the vertical distribution patterns of larvae in the coastal zone 18 km offshore north of the Newport transect (Figure 1). Thirty-two samples were taken within four depth strata (0-10, 11-50, 51-100, and 101-150

m) during a 24-h period in May 1972. Essentially, the entire water column was sampled. The volume of water filtered by each type of tow was about the same and the number of day and night tows in each stratum was equal. Because the nets had no opening-closing device, samples from all but the 0- to 10-m stratum were contaminated with catches from overlying waters. However, the maximum tow time spent outside the desired stratum was 20% for the deepest tows and was usually <10% for the intermediate depths. Therefore, no correction factor was applied to the data.

The greatest number of larvae and taxa was taken near the surface both day and night (Table 4). The 51- to 100-m stratum yielded the fewest larvae and taxa while the 11- to 50- and 101- to 150-m strata were intermediate. More larvae were taken at night, primarily in the 0- to 10-m stratum where avoidance during the day would be expected to be greatest. Mean larval length in this stratum was much greater at night which also indicated daytime avoidance by large larvae in surface waters. Mean larval length was also high in the 101- to 150-m stratum day and night, primarily because of the abundance of large osmerids there.

Of the 22 taxa taken, those represented by more than 10 larvae were examined for trends in distribution (Table 4). *Clupea harengus pallasi* (25-31 mm, $\bar{x}$ 28), *Ammodytes hexapterus* (17-37 mm, $\bar{x}$ 33), and *Ronquilus jordani* (6-21 mm, $\bar{x}$ 13) were concentrated in the upper 10 m at night and were completely absent in daytime collections from all depths. They exhibited strong daytime avoidance, indicated by night/day ratios. Large *Sebastes* spp. larvae (9-11 mm, $\bar{x}$ 10) were only taken at night and perhaps avoided by day, whereas small larvae (3-4 mm, $\bar{x}$ 4) were taken both day and night in the upper two strata. *Stenobrachius leucopsarus* (5-11 mm, $\bar{x}$ 8) and *Isopsetta isolepis* (14-23 mm, $\bar{x}$ 20) occurred predominantly in the upper two strata but showed no evidence of daytime avoidance. Mean larval lengths were about the same by day and night.

Of the remaining taxa, *Radulinus asprellus* (9-15 mm, $\bar{x}$ 12) appeared to occur throughout the water column in similar numbers and lengths during both day and night. Cyclopteridae spp. 1 (4-8 mm, $\bar{x}$ 5) occurred mainly near the surface in daytime but only in the 51- to 100-m stratum at night, possibly a result of patchiness or contamination of the deeper hauled net in the surface stratum. Only osmerids occurred primarily near the bottom (101-150 m), by day and night. Some were taken near the surface at night which may indicate vertical migration by some individuals or avoidance by day. Preliminary examination of specimens did not reveal the surface- and bottom-occurring osmerid larvae to be different species. Mean lengths for deep- and surface-caught osmerids were about the same, 21 and 23 mm.

ASSEMBLAGES

Two separate assemblages of fish larvae were distinguished, using a similarity coefficient matrix based on Sander's (1960) dominance-affinity index ($\sum$ lowest percent of all larvae in common between two stations). In 1971 a coastal assemblage occurred at stations 2 to 28 km offshore, which was distinct from another assemblage occurring at stations farther offshore (Figure 4). A similar pattern was found in 1972 during the 6 mo for which data were available. In 1971, the mean affinity value among stations 2, 6, 9, 18, and 28 was 65.81 and among stations 46, 56, 65, 74, 93, and 111 it was 60.61. In 1972, the mean affinity values for these same sets of stations were 43.21 and 56.61, respectively. *Sebastes* spp. were

TABLE 4.—Number/1,000m³, number of taxa, and mean length of fish larvae by day, night, and depth strata taken during a 24-h period 18 km off the mid-Oregon coast (lat. 45°04.0'N) in May 1972. N/D = night to day ratio. Each number is the sum of four replicate samples.

Depth strata (m)	*Clupea harengus pallasi*		Osmeridae		*Stenobrachius leucopsarus*		*Sebastes* spp.		*Radulinus asprellus*		Cyclopteridae spp. 1		*Ronquilus jordani*		*Ammodytes hexapterus*		*Isopsetta isolepis*		Other spp.		Total		No. taxa taken		Mean length (mm)	
	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N
0-10	0	46	0	4	9	3	3	10	7	1	14	0	0	29	0	22	31	8	14	8	78	131	13	13	13	21
11-50	0	1	0	1	0	4	1	2	3	5	3	0	0	0	0	0	12	12	5	5	24	30	9	9	15	15
51-100	0	2	0	0	0	0	0	0	3	2	0	8	0	0	0	1	1	1	2	0	6	14	3	5	11	12
101-150	0	1	21	13	0	0	0	0	2	5	0	0	0	0	0	1	3	2	1	3	27	25	4	8	20	20
Total	0	50	21	18	9	7	4	12	15	13	17	8	0	29	0	24	47	23	22	16	135	200	16	18	15	20
N/D		∞		0.86		0.78		3.00		0.87		0.47		∞		∞		0.49		0.73		1.48				

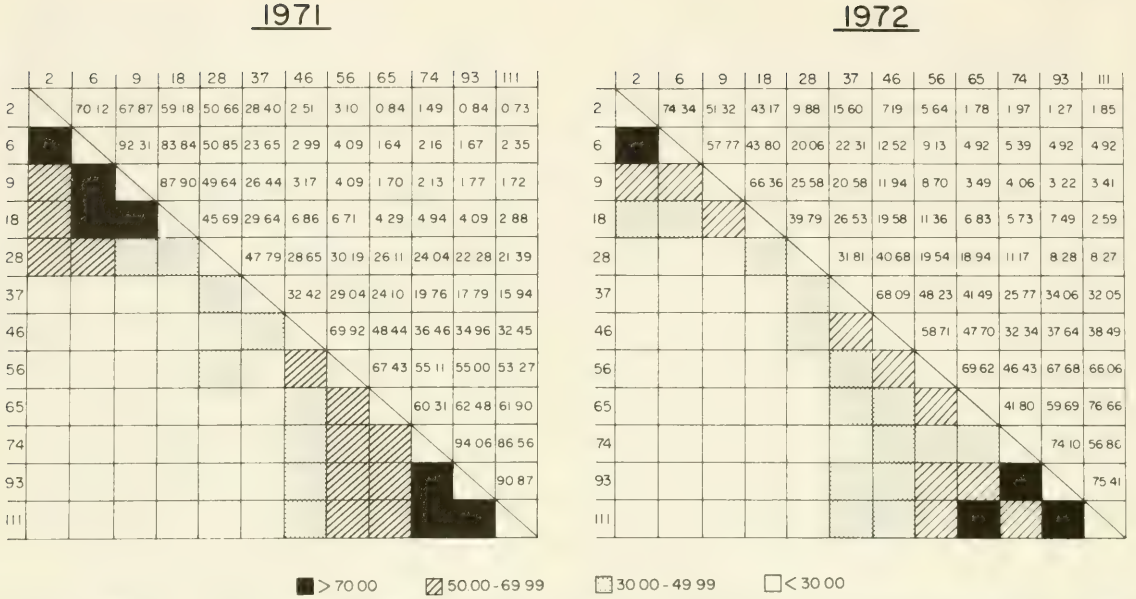

FIGURE 4.—Station to station similarity-coefficient matrices for 1971 and 1972 data on larval fishes based on Sander's (1960) dominance affinity index. All taxa except *Sebastes* spp. were included in the analysis.

excluded from the analysis to minimize masking effects that might have arisen because of the multispecies nature of the group. Since osmerids were known to be essentially coastal forms, they were not excluded.

Peaks in larval abundances were associated with the location of these two assemblages with an apparent transitional zone of low larval abundance between them (Figure 5). In both 1971 and 1972 abundance was relatively high inshore, dropped to a low at 28 km, and then increased seaward.

Larval taxa were determined to be associated with the coastal or offshore zone on the basis of whether 80% or more of all larvae were taken at stations 2 to 28 (coastal = C) or stations 37 to 111 (offshore = O). Using these criteria, 84 of the 90 taxa (93%) could be designated as coastal or offshore (Table 2). Fifty-three taxa in 16 families and 1 order were coastal. Of these, 49 were identified to species, 3 to family, and 1 to order. Ninety-nine percent of all larvae in these 53 taxa were taken in the coastal zone 2 to 28 km offshore. Thirty-one taxa in 15 families were offshore. Of these, 26 were identified to species, 4 to genus, and 1 to family. Ninety-six percent of all larvae in these 31 taxa were taken 37 to 111 km offshore.

Only six taxa could not be designated as coastal or offshore. This was probably due in part to rarity, e.g., *Hippoglossoides elassodon* (total standardized number = 5.29; 51% were C and 49% were O), *Bathyagonus* spp. (3.30; 47% C and 53% O), and to multispecies groups, e.g., Cyclopteridae spp. 1 (30% C and 70% O) and *Bathyagonus* spp. Interestingly, 96% of all *Sebastes* spp. larvae were taken in the offshore area. *Leptocottus armatus* was primarily coastal since 77% of all larvae were taken there. Only one sample outside the coastal area (Station 37, in February 1971) contained *L. armatus* larvae, but they were present in moderate numbers. *Hemilepidotus hemilepidotus* (67% C and 33% O) and *H. spinosus* (70% C and 30% O) distributions are more difficult to explain. *Hemilepidotus spinosus* larvae in the coastal area were smaller (4-9 mm, $\bar{x}$ 5.3) than those farther offshore (6-12 mm, $\bar{x}$ 8.9) as were *H. hemilepidotus* (4-6 mm, $\bar{x}$ 5.2 in the coastal area and 8-11 mm, $\bar{x}$ 9.3 offshore). *Hemilepidotus spinosus* larvae are sometimes abundant (>600 larvae/15 min tow) in the neuston (upper 15 cm of the water column), particularly at night (Richardson unpubl. data). These data suggest that larvae which are associated with surface waters may undergo some kind of offshore transport which does not affect nonneustonic species.

Modes of reproduction differ considerably between those species designated as coastal and those designated as offshore. Of the 53 coastal taxa

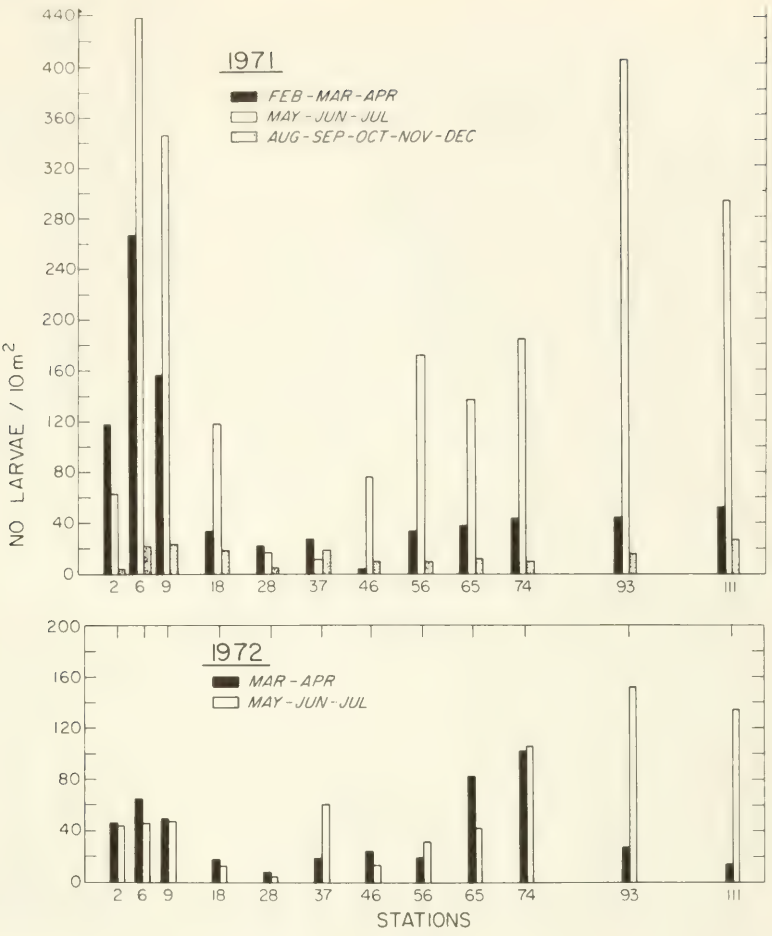

FIGURE 5.—Mean standardized abundance of fish larvae by station in 1971 and 1972.

(Table 2), 87% presumably come from demersal eggs (Breder and Rosen 1966) including all the osmerids, cottids, agonids, cyclopterids, and blennioids as well as *Clupea harengus pallasi, Ophiodon elongatus, Ronquilus jordani, Ammodytes hexapterus,* and *Clevelandia ios.* The eggs of *Microgadus proximus* are unknown but may also be demersal, as are those of *M. tomcod* in the Atlantic. Those not derived from demersal eggs, i.e., the six coastal flatfishes, come from small (~1 mm or less in diameter) planktonic eggs. Of the 31 offshore taxa, 81% presumably come from planktonic eggs. Eggs of the bathylagids, myctophids, bothids, and *Engraulis mordax* are probably all relatively small (~1 mm or less) whereas those of *Chauliodus macouni, Anoplopoma fimbria, Icosteus aenigmaticus, Atheresthes stomias, Embassichthys bathybius, Glyptocephalus zachirus,* and *Microstomus pacificus* are large, usually >2 mm. Eggs of *Tactostoma macropus, Icichthys lockington, Eopsetta jordani,* and *Lyopsetta exilis* are intermediate in size. Eggs of *Sebastolobus* spp., also of intermediate size, occur in floating masses rather than individually (Pearcy 1962). Larvae of the live-bearers *Brosmophycis marginata, Sebastes* spp., and possibly Ophidiidae sp. 1 are extruded. Of the offshore taxa, only *Hexagrammos* spp. and perhaps *Psychrolutes*-like sp. 1 come from demersal eggs.

Coastal Assemblage

One hundred thirty-nine samples were taken in the coastal assemblage, five at night, four at dusk or dawn, and the rest during daylight. All but four samples contained larvae, yielding 16,197 specimens or a standardized total [$\sum$ (number of larvae under 10 m² sea surface in each sample)] of 11,474.

Species Composition and Dominance

Seventy-three taxa assigned to 19 families and 1 order were taken in the coastal samples (Table 2). Of these, 62 were identified to species including unnamed numbered larval types considered to be distinct species, 7 to genus, 3 to family, and 1 to order. Margalef's (1958) formula for diversity ($D = S - 1/\ln N$, where S = number of species, N = total number of individuals), which provides a measure of species richness, yielded a value of 7.43 for the coastal assemblage, which was higher than that for the offshore assemblage.

Dominant taxa within the coastal assemblage were determined by a ranking method (Biological Index = BI) modified from Fager (1957), which takes into account both abundance and frequency of occurrence. By this method, the most abundant species in each sample is given five points, the next four, etc. Scores for each taxon are summed for all positive samples and divided by the total number of samples taken. The top 13 coastal dominants[15] (Table 5) accounted for 91.8% of the total larvae captured within 28 km of the coast over the entire sampling period. These same 13 taxa were also the 13 most abundant, although not always in the same order as dominance.

Osmerids were overwhelmingly the most dominant taxonomic group making up 50% of the total larval catch. They were the most abundant and most frequently taken larvae in the coastal assemblage. *Parophrys vetulus* and *Isopsetta isolepis* were also important in terms of abundance. These three taxa, together with fourth ranked *Microgadus proximus*, composed 78% of all larvae taken.

Seasonality

Obvious trends in seasonality were apparent from the 1971 data, which included samples from every month (Figure 6). Ninety-three percent of all larvae were taken during the 6-mo period from February through July. Two abundance peaks occurred within that period, one in February-March (24% of all larvae) before upwelling, and one in May-July (68% of all larvae) during the upwelling season. Larval abundance decreased greatly in August and remained low through December. Mean number of larvae under 10 m² was 142 in February-March, 202 in May-July, and

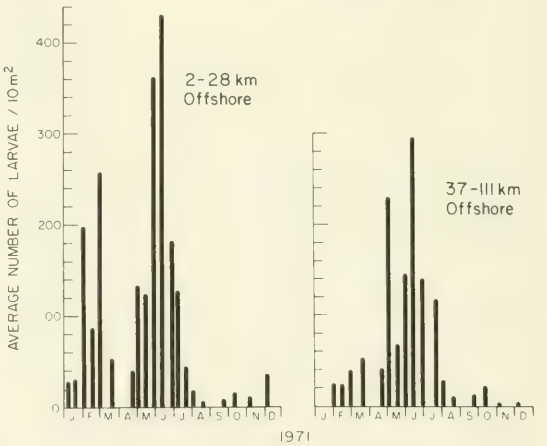

FIGURE 6.—Mean standardized abundance of fish larvae by cruise in 1971 in the coastal assemblage (stations 2 to 28) and the offshore assemblage (stations 37 to 111).

[15]Data on distribution and abundance of all 90 taxa will be available in an Oregon State University Sea Grant College Program Technical Report by the senior author in 1976-77.

TABLE 5.—Coastal dominants based on all larvae collected 2 to 28 km offshore in 1971 and 1972. [BI = Biological Index modified from Fager (1957)].

Taxa	BI	Rank order of abundance	Total standardized abundance[1]	% of total abundance	Positive tows out of 139	Total standardized abundance[1] Positive tows	Months of occurrence
1. Osmeridae	2.49	1	5,749.53	50.1	90	63.88	I-VIII, X-XII
2. *Parophrys vetulus*	1.41	2	1,479.59	12.9	60	24.66	I-VI, IX-XII
3. *Isopsetta isolepis*	1.39	3	1,157.90	10.1	71	16.31	I-VIII, X
4. *Microgadus proximus*	0.97	4	580.28	5.1	62	9.36	II-VIII
5. *Sebastes* spp.	0.77	9	180.66	1.6	57	3.17	I-XII
6. *Psettichthys melanostictus*	0.71	5	308.12	2.7	55	5.60	I-XI
7. *Artedius* sp. 1	0.50	7	189.26	1.6	66	2.87	I-VIII
8. *Platichthys stellatus*	0.39	8	187.40	1.6	30	6.25	III-VI, IX
9. *Lyopsetta exilis*	0.34	12	96.54	0.8	41	2.35	III-VIII
10. *Artedius* sp. 2	0.32	11	139.96	1.2	48	2.92	I-VIII
11. *Ammodytes hexapterus*	0.31	6	258.50	2.2	22	11.75	II-V
12. *Hemilepidotus spinosus*	0.29	13	69.04	0.6	21	3.34	I-III
13. *Cottus asper*	0.24	10	145.43	1.3	22	6.61	III-VII

[1]The sum of the standardized numbers (number under 10 m² sea surface) of larvae from each sample.

13 during August-December. Since samples were taken only during 6 mo in 1972 and larval abundances were greatly reduced, trends in seasonality could not be assessed.

In 1971, 42 taxa were taken in the February-March period and 46 taxa were taken from May to July. Of these, 10 occurred only during the winter period, 14 occurred only in the spring, and 32 were taken in both periods. Dominant taxa (with BI>1) in the February-March period were *P. vetulus* (BI = 4.09), *Ammodytes hexapterus* (BI = 1.76), *I. isolepis* (BI = 1.73), and Osmeridae (BI = 1.51). Together they made up 70% of the total larvae. *Parophrys vetulus* alone accounted for 44%. Dominant taxa from May to July 1971 were Osmeridae (BI = 4.12), *I. isolepis* (BI = 2.21), *M. proximus* (BI = 2.03), and *Lyopsetta exilis* (BI = 1.07). Together they made up 90% of the total number of larvae in those months. Osmerids accounted for 71% of the total in that period.

Thus the two abundance peaks in 1971 were not made up of completely different species. Some were common to both (Table 6). Some species occurred in the plankton collections during only a few months. For example, *Platichthys stellatus* larvae occurred over a restricted period of time (Table 6), small larvae were taken only during a few months mainly in spring, and they transformed and settled out at a small size (~8 to 9 mm). *Hemilepidotus spinosus* and *A. hexapterus* also were taken during a short-time period, primarily in winter. Larger *A. hexapterus* larvae avoid plankton nets and may have been present for a longer period than the data suggested. On the other hand, some species, such as *Parophrys vetulus* and *Psettichthys melanostictus*, occurred over a longtime period because of protracted spawning seasons and relatively long planktonic life (Table 6). *Parophrys vetulus* spawned primarily from January through March. Increases in larval lengths indicated that spawning stopped and larvae had settled out by July. Spawning began again in September and continued at least through December. Small larvae of *Psettichthys melanostictus* were taken in most months except July, August, and December. An increase in modal length occurred from June through August and again from September through November.

Other species showed trends in seasonal occurrence somewhere between the two extremes. *Isopsetta isolepis* apparently spawned from February through May. Modal lengths increased in successive months and large larvae were no longer available to our gear by August. *Microgadus proximus* also appeared to spawn from February through June and the larvae were not caught after August. *Lyopsetta exilis* apparently spawned from March through June and larvae were absent in collections from September through February. *Artedius* sp. 1 and *Artedius* sp. 2 were taken over an 8-mo period and small larvae occurred almost every month. *Cottus asper* was taken from February through July, but larval lengths showed no trends by month. Although taxonomic problems exist with the osmerids, two groups (possibly two species) were apparent from

TABLE 6.—Ranges and modal lengths (mm) for dominant fish larvae in the coastal assemblage (stations 2-28) in 1971. Asterisks indicate month in which average abundance per cruise was greatest. Parentheses are used where more than one modal peak occurred.

Taxa	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1A. Osmeridae (group 1)	5-6-10	6-11-21	15-19-24*	0	0	0	0	0	0	6-12	6	5-8-25
1B. Osmeridae (group 2)	0	0	4-6-11	0	5-15-32	7-25-35*	10-(24 27)-36	5-29-37	0	0	0	0
2. *Parophrys vetulus*	2-3-9	2-4-18*	3-8-21	4-(12 13)-18	5-8-22	14-21	0	0	2-3-6	2-10-17	3-5-14	2-5-14
3. *Isopsetta isolepis*	0	2-4-6	3-7-16	3-9-17	3-13-21*	6-16-21	10-11-19	0	0	2	0	0
4. *Microgadus proximus*	0	3-3-5	3-4-9	3-7-19	4-7-19	3-6-33*	6-16-24	14-(20 21)-31	0	0	0	0
5. *Sebastes* spp.	3-4-4*	3-3-4	3-4-4	4-4-7	3-4-5	4-4-9	16	3-(3 4)-17	3-3-14	0	9	6
6. *Psettichthys melanostictus*	3	2-3-4	5	5	3-13-23*	5-6-23	8-11-21	14-22	4-(4 5)-8	2-9-13	3-11-26	0
7. *Artedius* sp. 1	2-3	2-3-4*	3-(8 10)-10	4-(4 5)-9	3-6-13	4-7-12	4-6-12	3-(10 11)-11	0	0	0	0
8. *Platichthys stellatus*	0	0	3-3-5	3-4	3-7-9*	5-7-9	0	0	3	0	0	0
9. *Lyopsetta exilis*	0	0	5	4-4-7	4-5-11	5-10-21*	9-11-21	11-19	0	0	0	0
10. *Artedius* sp. 2	2-3	2-4-6	2-6-9*	[illegible]	3-6-13	3-3-13	6-7-10	3-4-9	0	0	0	0
11. *Ammodytes hexapterus*	0	4-4-9	4-10-19*	14-19	11-12	0	0	0	0	0	0	0
12. *Hemilepidotus spinosus*	5-5-8	4-5-6	4-5-6*	0	0	0	0	0	0	0	0	0
13. *Cottus asper*	0	5	4-5-8*	0	6-9-9	5-6	6-7-9	0	0	0	0	0

length-frequency data (Table 6). Two distinct length modes occurred in March, which suggested the presence of both a winter-spawned and a spring-spawned group.

Distribution Trends

Peak abundances for dominant species within the coastal assemblage generally occurred at stations 6 and 9 (Figure 7) for those larvae that were most abundant before the usual months of upwelling (e.g., *P. vetulus, Ammodytes hexapterus*) and also for those most abundant during the upwelling season (e.g., Osmeridae, *I. isolepis, M. proximus*). Abundance usually decreased toward the coast and farther offshore. However, on two winter cruises, osmerids were most abundant at the 2-km station. A few species, such as *C. asper*, were always most abundant at the 2-km station, and numbers decreased with distance from shore. *Cottus asper* is known to spawn in Yaquina Bay where it is the third most abundant larval species (Pearcy and Myers 1974). It is found in greatest numbers in the upper part of the Bay, and its occurrence offshore probably is a result of tidal flushing.

Year to Year Variation

The mean standardized number of larvae per station during the winter and spring-summer periods was considerably higher in 1971 than in

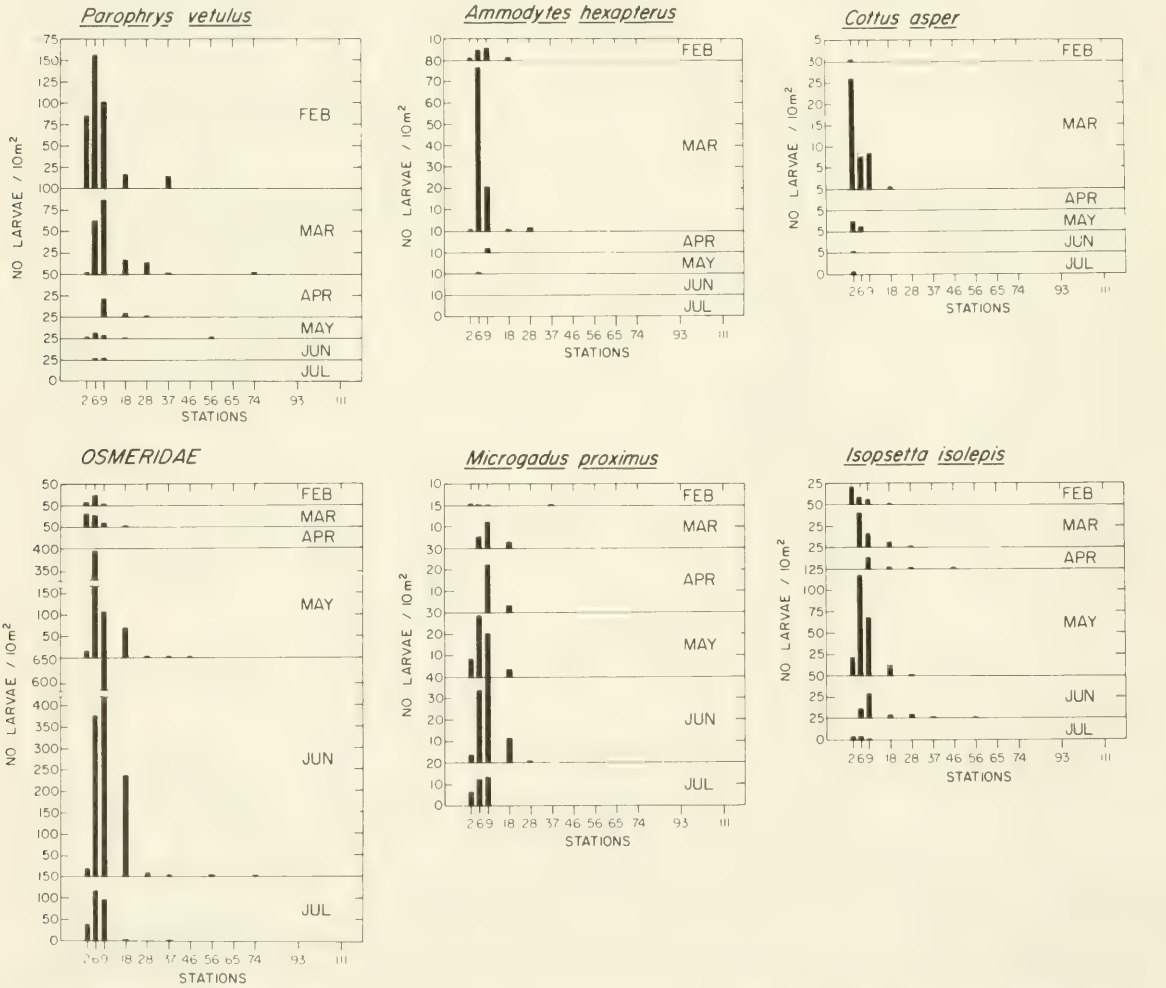

FIGURE 7.—Distribution patterns of fish larvae in the coastal assemblage (stations 2 to 28) during months of peak abundance in 1971. Abundances are monthly means.

1972, sometimes by an order of magnitude (Figure 5). These differences are exemplified further by the mean standardized number of larvae per tow (Table 7).

In March-April, five of the six dominant (BI ≥ 1) taxa were more abundant in 1971 than 1972 (Table 7). The exception was *Sebastes* spp., which was 6.5 times more abundant in 1972 based on mean standardized number per tow. The greatest decrease occurred for *P. vetulus*, which was 24.9 times more abundant in 1971. The low numbers of *P. vetulus* in 1972 may have been partly due to an early spawning; small larvae were taken as early as September and October 1971 (Table 6) and many larvae may have settled out by the March-April 1972 period. Or 1972 may have been a year of reduced larval survival for *P. vetulus*. *Ammodytes hexapterus* was also more abundant in 1971 with 12.2 times more larvae being taken than in 1972. Dominance shifted from *P. vetulus* in 1971 to the Osmeridae in 1972 even though osmerids were less abundant in 1972 than 1971. The number of taxa taken was similar each year although the species richness value was higher in 1972 (Table 7).

During the May-July period, the five dominant taxa were all more abundant in 1971 than in 1972 (Table 7). The largest decline occurred in *M. proximus* where 13.5 times more larvae were taken in 1971. Osmerids were 10.6 times more abundant in 1971. Their decline in numbers had a major impact on overall abundance in 1972. In 1971, an average of 143 osmerids were taken per tow and they contributed 71% to the total larval abundance. While still the dominant taxon in May-July 1972, they were less abundant and made up 57% of the total. Considerably fewer taxonomic groups were taken in 1972. This may have been a result of fewer samples taken and a corresponding reduction in numbers of rare taxa.

TABLE 7.—Comparison of data on larval fishes collected off Oregon in 1971 and 1972.
[BI = Biological Index modified from Fager (1957)].

Taxa (dominants listed separately)	No. samples		BI		Mean no./10 m²			% total abundance		Species richness ($D = S - 1/\ln N$)	
	1971	1972	1971	1972	1971	1972	1971/1972	1971	1972	1971	1972
March-April 2-28 km	12	22								5.24	6.41
Parophrys vetulus			4.25	<1	31.13	1.25	24.90	26.6	4.0		
Isopsetta isolepis			1.85	1.63	12.17	3.16	3.85	10.4	10.1		
Ammodytes hexapterus			1.68	<1	16.83	1.38	12.20	14.4	4.4		
Microgadus proximus			1.25	<1	5.59	2.12	2.64	4.8	6.8		
Osmeridae			<1	2.00	11.41	8.50	1.34	9.7	27.2		
Sebastes spp.			<1	1.39	0.33	2.13	0.16	0.3	6.8		
All other species			—	—	39.69	12.72	3.12	33.9	40.7		
Total (41 in 1971; 48 in 1972)			—	—	117.14	34.82	3.36	100.1	100.0		
May-July 2-28 km	34	20								4.94	3.30
Osmeridae			4.12	3.33	143.23	13.51	10.60	70.8	57.4		
Isopsetta isolepis			2.21	1.88	23.10	2.85	8.10	11.4	12.1		
Microgadus proximus			2.03	<1	12.59	0.93	13.54	6.2	4.0		
Lyopsetta exilis			1.07	<1	2.31	0.37	6.24	1.1	1.6		
Artedius sp. 1			<1	1.03	2.04	0.86	2.37	1.0	3.6		
All other species			—	—	18.99	5.02	3.78	9.4	21.3		
Total (46 in 1971; 24 in 1972)			—	—	202.14	23.55	8.59	99.9	100.0		
March-April 37-111 km	16	20								2.52	2.48
Sebastes spp.			3.97	4.32	26.05	29.12	0.89	58.7	85.9		
Stenobrachius leucopsarus			2.53	1.20	8.48	1.90	4.46	19.1	5.6		
Tarletonbeania crenularis			1.34	<1	2.94	0.54	5.44	6.6	1.6		
Hemilepidotus spinosus			<1	1.30	0.48	0.93	0.52	1.1	2.7		
All other species			—	—	6.43	1.41	4.56	14.5	4.2		
Total (16 in 1971; 16 in 1972)			—	—	44.40	33.80	1.31	100.0	100.0		
May-July 37-111 km	38	28								3.66	3.35
Stenobrachius leucopsarus			3.10	2.82	76.78	15.11	5.08	43.8	19.6		
Sebastes spp.			3.08	3.50	56.50	22.55	2.51	32.2	29.3		
Lyopsetta exilis			1.96	<1	10.99	4.78	2.30	6.3	2.3		
Tarletonbeania crenularis			1.47	1.11	9.56	4.84	1.98	5.4	6.3		
Engraulis mordax			<1	2.00	4.68	28.06	0.17	2.7	36.4		
All other species			—	—	16.79	4.74	3.54	9.6	6.2		
Total (32 in 1971; 25 in 1972)			—	—	175.30	76.98	2.27	100.0	100.1		

The species richness value in 1972 (Table 7) was lower than in 1971, indicating that fewer species were present.

Offshore Assemblage

During the sampling period, 148 samples were taken (45 at night, 14 at dusk or dawn, 89 in daylight) in the offshore assemblage. The 141 positive samples yielded 7,381 larvae or a standardized total [Σ (number of larvae under 10 m^2 sea surface in each sample)] of 10,868.

Species Composition and Dominance

Fifty-two taxa in 21 families were taken in the offshore samples (Table 2). Of these, 43 were identified to species, 6 to genus, and 3 to family. The species richness value, based on Margalef's (1958) formula for diversity, was 5.73 for the offshore assemblage, which was lower than the value of 7.43 for the coastal assemblage.

The top 10 dominant (BI) taxa (see footnote 15) in the offshore assemblage accounted for 94.3% of the total number of larvae in this assemblage (Table 8). Nine of these 10 taxa also were among the 10 most abundant although in different order, with *Microstomus pacificus* (total standardized abundance 81.74) replacing *Hemilepidotus spinosus*.

The two major dominants were *Sebastes* spp. and *Stenobrachius leucopsarus,* which together accounted for 70% of all larvae taken offshore. *Tarletonbeania crenularis* and *Lyopsetta exilis* were also dominant in the offshore assemblage in terms of overall abundance and frequency of occurrence. Fifth ranked *Engraulis mordax* occurred in concentrations (standardized numbers per positive tow) equivalent to *Sebastes* spp. and *Stenobrachius leucopsarus* (Table 8) although it was less frequently taken. The top six dominant taxa composed 91% of the total larval abundance compared with 13 taxa contributing that percentage in the coastal area.

Seasonality

In 1971, 94% of all larvae were taken between February and July, as in the coastal area, and 83% were taken during the 3-mo period from May to July (Figure 6). The winter (February-March) peak of abundance noted in the coastal area was absent offshore. Larval abundance decreased in August and remained low for the rest of the year. The minor increase in numbers in October was solely due to small *Citharichthys* (probably *sordidus*) larvae 37 to 46 km offshore. Since only 5 mo of data were available for the offshore assemblage in 1972, seasonal trends could not be assessed.

Dominant taxa (BI>1) within the May-July peak abundance period in 1971 were essentially the same as those (Table 8) for the entire 1½-yr sampling period. These were *S. leucopsarus* (BI = 3.10), *Sebastes* spp. (BI = 3.08), *L. exilis* (BI = 1.96), and *T. crenularis* (BI = 1.47). Together they made up 88% of the total larvae taken in that spring-summer period.

As in the coastal zone, some taxa had restricted spawning periods and their larvae were present in the plankton for a relatively short time, e.g., *E. mordax* and *L. exilis* (Table 9). Both species showed distinct growth trends. *Hemilepidotus spinosus* was also present during a short period although the larvae in the offshore zone were usually larger than those in the coastal area (Table 6). *Glyptocephalus zachirus* was taken as small larvae only in April to June indicating a rather restricted spawning period, but large larvae were present through September. The larvae grow

TABLE 8.—Offshore dominants based on all larvae collected 37 to 111 km offshore in 1971 and 1972. [BI = Biological Index modified from Fager (1957)].

Taxa	BI	Rank order of abundance	Total standardized abundance[1]	% of total abundance	Positive tows out of 148	Total standardized abundance[1] Positive tows	Months of occurrence
1. *Sebastes* spp.	3.24	1	3,967.82	36.5	112	35.43	I-XII
2. *Stenobrachius leucopsarus*	2.28	2	3,648.00	33.6	87	41.93	I-X
3. *Tarletonbeania crenularis*	1.27	4	635.20	5.8	64	9.92	II-X, XII
4. *Lyopsetta exilis*	0.73	5	475.23	4.4	41	11.59	V-VIII
5. *Engraulis mordax*	0.67	3	1,000.70	9.2	25	40.03	VI-VIII
6. *Protomyctophum thompsoni*	0.67	6	173.77	1.6	52	3.34	III-XII
7. Cyclopteridae spp. 1	0.51	10	79.70	0.7	38	2.10	II-IX
8. *Glyptocephalus zachirus*	0.26	8	113.81	1.0	27	4.21	III-IX
9. *Hemilepidotus spinosus*	0.22	13	29.78	0.3	12	3.26	II-IV
10. *Bathylagus ochotensis*	0.19	7	131.46	1.2	31	4.24	III-VIII

[1]The sum of the standardized numbers (number under 10 m^2 sea surface) of larvae from each sample.

TABLE 9.—Ranges and modal lengths (mm) for dominant fish larvae in the offshore assemblage (stations 37 to 111) in 1971. Asterisks indicate month in which average abundance per cruise was greatest. Parentheses are used where more than one modal peak occurred.

Taxa	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1. *Sebastes* spp.	3-5-5	3-4-9	6-7-7	3-4-8*	3-4-20	3-4-14	3-3-8	3-14	2-3-14	0	3-5-5
2. *Stenobrachius leucopsarus*	4-5-5	4-5-7	4-6-6	3-7-17	4-7-18*	4-9-15	5-(7 8 9)-16	7-13-14	9-10-15	0	0
3. *Tarletonbeania crenularis*	7-11	5-11-15	11-15	8-12-16	4-8-20*	3-(7 8)-17	5-8-17	9-10-15	4-11	0	9-10
4. *Lyopsetta exilis*	0	0	0	3-5-17*	4-14-19	5-14-21	15-(19 22)-22	0	0	0	0
5. *Engraulis mordax*	0	0	0	0	[illegible]	4-5-16*	4-10-25	0	0	0	0
6. *Protomyctophum thompsoni*	0	3-(3 8)-13	0	6-13-18*	5-11-16	11-13	8-12-17	5-14-16	5-14-18	8	5-14
7. Cyclopteridae spp. 1	4-5-5*	9	14	5-20	5-11	11	6-14-14	15-19	0	0	0
8. *Glyptocephalus zachirus*	0	0	8-8-9	4-8-20*	4-54	45	32	67	0	0	0
9. *Hemilepidotus spinosus*	6*	7-10-10	0	0	0	0	0	0	0	0	0
10. *Bathylagus ochotensis*	0	5-6-20	9	5-(5 11)-22	4-11-30*	15-24	13-22	0	0	0	0

quite large (>40 mm) before metamorphosis and have an extended pelagic life (Pearcy et al. 1977). Some taxa were taken throughout most of the year and showed no strong evidence for a definite spawning period, e.g., the multispecies group *Sebastes* spp., *T. crenularis,* and *Protomyctophum thompsoni* (Table 9). Intermediate to these were species which occurred over a rather long period but did show some indication of seasonality based on larval lengths, e.g., *Stenobrachius leucopsarus* and *Bathylagus ochotensis.* Cyclopteridae spp. 1 was taken over a long time period from February through September. No trends in growth were evident probably because it is a multispecies group.

Distribution Trends

Peak abundances occurred 46 to 65 km offshore for some species, e.g., *L. exilis, G. zachirus,* and some *Sebastes* spp. (Figure 8). Spawning presumably took place near the outer shelf-upper slope region where depths were ~200-300 m. *Sebastes* spp. also had an abundance peak further offshore, possibly the result of offshore drift of larvae.

A more oceanic distribution was characteristic of larvae of mesopelagic fishes such as the myctophids *Stenobrachius leucopsarus, T. crenularis,* and *P. thompsoni* (Figure 8). Peak abundances occurred at the 74- to 111-km stations with a decline in abundance toward the coast, although a few myctophid larvae were taken over the shelf at 18 to 28 km offshore.

Larvae of *E. mordax* occurred in large numbers (147/under 10 m²) only once in 1971, at the 65-km station in July. In 1972, peak abundance also occurred in July but at 74, 93, and 111 km offshore (236, 297, and 124/under 10 m², respectively). These peaks may be associated with spawning in the relatively warm waters of the Columbia River plume (Richardson 1973).

Year to Year Variation

In March-April, no major differences in abundance or species richness occurred between 1971 and 1972 (Figure 5, Table 7). The dominant taxa were reasonably similar, although there was some decline in abundance in *S. leucopsarus* and *T. crenularis* and some increase in *Sebastes* spp. and *Hemilepidotus spinosus* in 1972.

In the May-July period, however, mean larval abundance was higher in 1971 (Figure 5, Table 7). Four of the five dominant taxa were more abundant in 1971. A major decline occurred in *S. leucopsarus* catches in 1972. A major increase in abundance occurred in *Engraulis mordax* in 1972; six times more larvae were taken than in 1971. This may have been due to increased sampling in Columbia River plume water (Richardson 1973). Species richness values were similar in both years.

DISCUSSION

Coastal and Offshore Larval Fish Distributions

There was a marked inshore-offshore separation of larval fish assemblages. Little overlap in distribution occurred between coastal and offshore larvae. Most (99%) larvae designated as coastal were collected within 28 km of shore and most (96%) larvae designated as offshore were found beyond 28 km. The 28-km station consistently had low larval abundances (Figure 5) and appeared to be a transitional zone between coastal and offshore waters. The biomass of fishes, shrimps,

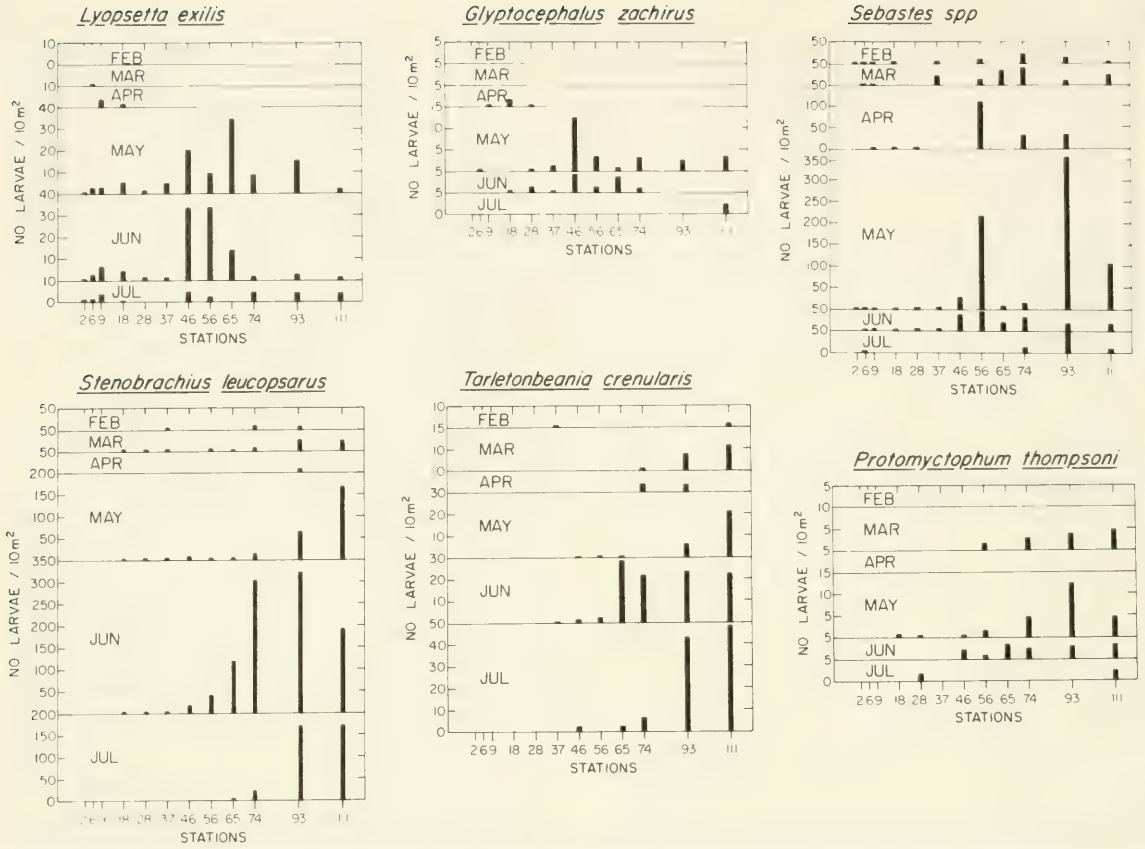

FIGURE 8.—Distribution patterns of fish larvae in the offshore assemblage (stations 37 to 111) during months of peak abundance in 1971. Abundances are monthly means.

and cephalopods caught in plankton nets and mid-water trawls was also low at this station compared with offshore stations (Pearcy 1976). Interestingly, this region is located over midshelf where water depth is about 95 m rather than at the shelf break.

Explanations for this observed phenomenon are severalfold. Certainly peak concentrations of coastal and offshore larvae are related in part to the spawning location of adults. Most larvae that are taken in plankton collections are small, have not been in the water column for an extended period of time, and thus occur near the area in which they were spawned. Possibly few adult fish spawn near 28 km offshore although data to substantiate this are not available.

Circulation patterns also help to explain the observed larval distributions. General seasonal trends of currents over the continental shelf, shoreward of the California Current, have been described by Smith et al. (1971), Wyatt et al. (1972), Huyer (1974), Smith (1974), Huyer et al. (1975), and others. The predominant currents, those of greatest velocity, are alongshore. In winter, October through February, when winds are predominantly from the southwest, the main flow is northward (Davidson Current) at all depths, with an onshore drift component at the surface. A strong alongshore flow occurs within 28 km of the coast. In summer, May through August, winds are predominantly from the northwest and the main current flow is southward, with an offshore drift component at the surface. Southward flow is greatest in a coastal jet located 15 to 20 km offshore. In spring, deeper water (bottom third of the water column) flows south but at a slower speed than the surface water (upper third of the water column). In summer, this deeper water flows northward. There is also a shoreward drift component in these deeper and intermediate waters which produces upwelling, a process which taken place mainly within 10 to 20 km of the coast.

Spring (March, April) and fall (September) are usually periods of transition with variable winds and currents. Since the predominant currents are north-south (perhaps 10 times stronger than east-west), transport of larvae is also predominantly north-south rather than inshore-offshore. Thus, the greatest concentrations of larvae spawned in the coastal and offshore areas would be retained along zones parallel to the coast. Perhaps the strong north or south flow (coastal jet) reported to occur around 15 to 28 km offshore serves as some kind of barrier to inshore or offshore transport of larvae. The presence of an actual persistent front in this region, which would help explain the faunal break at 28 km, has not been demonstrated. The strongest front that has been observed in this region is associated with Columbia River Plume water, which flows south off Oregon in summer. However, its position is not stable and it is not present off Oregon in winter. The presence of a surface front around 28 km offshore has been demonstrated during upwelling when upward sloping isopycnals break the surface. This occurs only during upwelling, usually in summer.

The extent of north-south transport is unknown. However, evidence suggests that shoreward of 11 km, because of current reversals, the mean north-south current velocity (alongshore flow) may be approximately zero over the summer (Huyer 1974; Huyer et al. 1975) and possibly also over the winter (Huyer pers. commun.). Thus, at least in the coastal zone, circulation patterns may explain maintenance of larvae in specific areas with respect to north-south as well as inshore-offshore. If this apparent retention of coastal larvae in the coastal area is persistent with respect to north-south and east-west transport, it would seem that other factors, most notably food, may be more critical to early survival than transport away from favorable areas (Hjort 1926). We have no evidence that predators of fish eggs and larvae are concentrated at the 28-km station (Pearcy 1976).

Comparison of Coastal Larvae With Yaquina Bay Larvae

Similarities exist between the species composition of fish larvae in the coastal area and in Yaquina Bay (Pearcy and Myers 1974). The cottids and the pleuronectids were the most speciose families in both areas (not considering the potential number of *Sebastes* spp.). Families in the Bay not represented offshore were Gobiesocidae, Gasterosteidae, and Syngnathidae. Families from the coastal region not represented in the Bay were Myctophidae, Anoplopomatidae, Bathymasteridae, and Clinidae.

Larval distributions described by Pearcy and Myers (1974) as "bay" or "offshore" are generally supported by the present study. Major differences in dominant taxa were found between the Bay fauna and the coastal assemblage in this paper. The two most abundant Bay species, which accounted for 90% of all larvae, were either not taken in the coastal assemblage, i.e., *Lepidogobius lepidus,* or were relatively uncommon, i.e., *Clupea harengus pallasi.* The only goby taken in the coastal assemblage was *Clevelandia ios,* which was designated Gobiidae type 1 from the Bay. Two of the three taxa listed by Pearcy and Myers (1974) as "bay only" types, *Lumpenus sagitta* and *Anoplarchus* spp., were taken in the coastal assemblage. The most abundant larvae in the coastal assemblage, Osmeridae, *Parophrys vetulus, Isopsetta isolepis,* and *Microgadus proximus,* did not contribute significantly to the larval fish fauna of Yaquina Bay.

Seasonal patterns of larval abundance were similar in both areas with the peak occurring February to June in the Bay and February to July in the coastal area. The egg abundance peak of July to October in the Bay, which was primarily attributed to northern anchovy, *Engraulis mordax,* corresponds somewhat with the peak abundance of anchovy larvae offshore in this study. The eggs may have been spawned in the Bay or carried into the Bay from coastal areas. Whichever is the case, the fact that anchovy larvae were not abundant in the Bay indicates development there was unsuccessful. Additional evidence for the lack of developmental success of anchovy eggs and larvae in northern estuarine areas was given by Blackburn (1973). Anchovy eggs were taken in plankton collections in Puget Sound from May through August during a year-long survey. Larvae were never captured in ½-m plankton nets (0.5-mm mesh), but a few anchovy larvae (presumably large) and juveniles were captured in larger tow nets (3 × 6 m mouth diameter, 6-mm mesh cod end and 1 × 2 m mouth diameter, 3-mm mesh cod end). In another year-long study in the Columbia River estuary (Misitano 1977), only large (22-55 mm) anchovy larvae were taken in low numbers from October through March. Similarly, anchovy larvae were rare in

Humboldt Bay (Eldridge and Bryan 1972). Data from this study and Richardson (1973; unpubl. data) provide evidence that at least off Oregon major anchovy spawning occurs and early development is successful offshore beyond 28 km rather than in coastal areas.

Pearcy and Myers (1974) reported Yaquina Bay was an important spawning area only for *Clupea harengus pallasi* and numerous cottids, gobies, and stichaeids. It was, however, an important nursery area for juvenile *Parophrys vetulus, Hypomesus pretiosus, Platichthys stellatus, Citharichthys stigmaeus,* and embiotocids. The present study has shown that the coastal area 2 to 28 km offshore is important as a spawning area for *P. stellatus* and *Parophrys vetulus* which utilize Yaquina Bay estuary during part of their early life.

Comparison With Other Planktonic Components

Results from studies on zooplankton (Peterson and Miller 1975, see footnote 2), pink shrimp, *Pandalus jordani,* larvae (Rothlisberg 1975), and crab larvae (Lough 1975) off Oregon indicate that trends in seasonality and inshore-offshore distribution do not always correspond with those found for fish larvae. These planktonic components were all studied from the same sets of samples (70- and 20-cm bongos, 0.571- and 0.233-mm mesh nets, collected from June 1969 to August 1972 off Newport).

Seasonal abundance peaks of certain components of the meroplankton, i.e., larvae of shrimp, crabs, and fishes, appear to be similar but do not correspond as well with those of zooplankton. Total zooplankton (predominantly copepods) abundance in the coastal zone is high in summer during upwelling, with peaks usually in late June and July, and low in winter (November-January). A secondary winter-spring peak may develop around February-April, but it is an order of magnitude lower than the summer peak. Larvae of the pink shrimp first occur in March and are in the plankton through June. Larvae of most species of crabs occur between February and July with peak abundances in May and June, although a few species are present all year; lowest abundances are in December and January. Fish larvae are most abundant between February and July. Those larvae that are present during the summer zooplankton peaks tend to be of advanced developmental stages. Since the 0.233-mm mesh used for zooplankton did not adequately sample smaller animals such as copepod nauplii, it may be that peak abundances of such potential food items actually coincide with larval abundance peaks.

Inshore-offshore distribution trends appear to differ among the various planktonic constituents with crab larvae being most similar to fish larvae. Total zooplankton abundance, which is influenced mainly by copepods, is consistently greatest (often by an order of magnitude) in both summer and winter at the 2-km station, grades to lows at 18 km; and according to Cross (1964), copepod abundances continue to decrease farther from shore. However, within the coastal zone (2-18 km) abundance of individual species may not follow that pattern, e.g., some may be more abundant offshore of 2 km. Larvae of the pink shrimp first occur (March) within 37 km of shore with greatest concentrations at 9 to 28 km. Later (April-May) the larvae are much more widely dispersed, occurring from 2 to 111 km; abundance peaks may occur coastally at 9 km as well as offshore at 93 km. Later in the season (June) when they are ready to settle, peak abundances occur around 28 to 46 km offshore, apparently over favorable settling areas. Larvae of most species of crabs which are coastal forms as adults occur within 18 km of the coast. Highest densities are at 2 and 6 km with a dramatic decrease between 9 and 18 km. Larvae of slope species occur primarily in the offshore area beyond 28 km. These distributions are similar to the coastal and offshore distributions of larval fishes. However, larvae of a few crab species which are coastal as adults are found at all stations from 2 to 111 km and are abundant in the coastal area as well as offshore. Larvae of at least one of these species, *Cancer oregonensis,* have been found in great abundance (~11 liters of megalopa in one 15-min night surface tow) in the neuston 65 km offshore (Richardson unpubl. data). This type of distribution is similar to that found for larvae of the fish *Hemilepidotus spinosus,* which are also neustonic. This apparent offshore transport of larvae spawned in the coastal zone inside 28 km suggests that those which spend at least part of their early life in surface waters may be subjected to different dispersal mechanisms than those which do not occur in the neuston. Offshore flow of surface waters occurs during the upwelling season, providing a mechanism of transport.

Comparison to the Northeast Pacific

Direct comparisons between results from this study and most previous reports on larval fishes in the northeast Pacific with respect to species composition, seasonality, and inshore-offshore distribution patterns are difficult to make for several reasons. Cruise tracks differed with respect to distance of stations from shore and proximity of stations to each other. Duration of sampling effort and types of gear used were not the same. Aron's (see footnote 4) data came from mid-water trawl samples taken on long oceanic cruise tracks between southern California and southwest Alaska from July through October. LeBrasseur's (see footnote 7) report was based on mid-water trawl and NORPAC net collections taken in the northeast Pacific at a broad array of stations from 1956 to 1959. Waldron's (1972) results, excluding Puget Sound, came from meter net collections made in a grid pattern with transects on each degree of latitude between 42° and 51° (Oregon to British Columbia) and stations extending from the 55-m isobath to 550 km offshore. His samples covered only a 1-mo period in April and May. Naplin et al. (see footnote 8) reported on samples collected with 60-cm bongos along three widely spaced transects off Washington and British Columbia in October and November. Richardson's (1973) data came from 70-cm bongo, meter net, and mid-water trawl samples collected off Oregon at a wide array of stations from May to October. However, some trends are evident.

The most abundant, most dominant, and most frequently taken taxa in the above mentioned studies (which included few or no samples from nearshore areas) were myctophids, mainly *Stenobrachius leucopsarus, Tarletonbeania crenularis,* and sometimes *Protomyctophum thompsoni* (and *Diaphus theta* in southern areas), and scorpaenids, mainly *Sebastes* spp. (particularly over shelf and slope areas). This is similar to the offshore assemblage in this study. Richardson (1973) also found *Engraulis mordax* to be important as it was in our offshore assemblage. Those studies which included samples from shelf areas showed increased importance of pleuronectid larvae, e.g., *Isopsetta isolepis, Parophrys vetulus, Platichthys stellatus,* and *Psettichthys melanostictus* (Waldron 1972). None of the above studies included intensive sampling in the nearshore zone (e.g., within 9 km of the coast) to allow detailed comparison with our coastal assemblage. However, Aron (1959) stated that large numbers of capelin, *Mallotus villosus,* larvae were taken in northerly inshore waters. Also, osmerids and *Ammodytes hexapterus* were among the 10 most abundant larvae taken in Waldron's (1972) samples. Richardson (1973) showed that osmerid larvae were taken in moderate numbers at nearshore stations although they were not top dominants when all samples were combined. More recent samples from 12 transects 2 to 56 km off Oregon (Laroche and Richardson[16]) have shown that osmerids, *Parophrys vetulus, I. isolepis, Microgadus proximus,* and some cottids are dominant in the coastal waters from the Columbia River to Cape Blanco in spring months, which is similar to our coastal assemblage.

The only available information on seasonality based on one or more years of data was presented by LeBrasseur (see footnote 7). The greatest number of larvae per sample (1.0) was taken in the March-May quarter, with 0.3 in June-August, 0.1 in September-November, and 0.05 in December-February. The May-October data discussed by Richardson (1973) showed an abundance peak in May in 1-m net samples and a peak in July-August in bongo and mid-water trawl samples with low abundances after August. The data of Naplin et al. (see footnote 9) showed low abundances (except for myctophids) and low numbers of species in October-November. These trends are similar to those found in this study.

No previous studies have demonstrated actual coastal and offshore assemblages of fish larvae although mention has been made of a break in species composition, abundance, and frequency of occurrence between shelf and oceanic areas. Aron (1959) stated that, in oceanic regions, the larvae of inshore fishes disappeared and myctophid larvae became common. LeBrasseur (see footnote 7) indicated larvae were taken in 5% of the samples within 100 miles of the coast but in only 1% of the samples from farther offshore. Waldron (1972) reported a greater number of larvae were taken inside the 914-m isobath than beyond it. More recent data (Laroche and Richardson see footnote 16) have shown that coastal and offshore assemblages of fish larvae, similar to those described in this paper for the mid-Oregon coast, occur along

[16]Laroche, J. L., and S. L. Richardson. Spring patterns of larval fish distributions from the Columbia River to Cape Blanco, Oregon, 1972-1975, with emphasis on English sole, *Parophrys vetulus.* Manuscr.

the entire Oregon coast from the Columbia River to Cape Blanco at least in spring (March-April). Thus it seems likely that similar species composition, seasonality, and inshore-offshore assemblages of larval fishes may occur over a much broader shelf-slope area in the northeast Pacific.

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BIOLOGY OF OFFSHORE HAKE, *MERLUCCIUS ALBIDUS*, IN THE GULF OF MEXICO[1]

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ABSTRACT

Biological data of the offshore hake, *Merluccius albidus*, in the Gulf of Mexico are presented and compared with those of other species of *Merluccius*. The species has been found from Georges Bank to Rio de Janeiro, Brazil, in 192 to 1,170 m. In the Gulf of Mexico it occurs in greatest abundance in the De Soto Canyon area in depths of 350 to 1,000 m.

Merluccius albidus are segregated by size and sex on the continental slope with juveniles, males, and young females found in depths less than 550 m and large, mature females found in depths exceeding 550 m. Mature males were smaller than females and grew at a reduced rate following the onset of sexual maturity.

Males and young females were found on the upper slope and older mature females found on the lower slope. Spawning appeared to take place on or near the bottom in 330 to 550 m. Spawning in the southern latitudes appears to occur from late spring to early fall and may be more protracted at the southern limits of its range. Eggs and the earliest larval stages have been described only for *M. albidus* from New England.

Merluccius albidus are opportunistic feeders preying primarily on fishes, squid, and crustaceans. Fishes make up about 75% of their diet, with species of Merlucciidae and Myctophidae consumed most frequently. Prey species exhibited diel movement, but the similarity between day and night catch rates of *M. albidus* suggests that offshore hake do not move far off the bottom in pursuit of prey.

Density estimates suggested a small population of *M. albidus* in the northern Gulf of Mexico. *Merluccius albidus* stocks in 370 to 730 m on the De Soto Canyon slope north of Tampa, Fla., are estimated to be a minimum of 3.3×10^6 kg.

Species of the genus *Merluccius* are distributed worldwide in temperate and tropical waters but are exploited primarily in temperate seas. Aspects of their biology, distribution, and utilization have been reported by numerous authors (Hickling 1927, 1933; Bigelow and Schroeder 1953, 1955; Graham 1956; Fritz 1960; Lozano Cabo 1965; Marak 1967; Botha 1969, 1971; Grinols and Tillman 1970; and Nelson and Larkins 1970). Northern Gulf of Mexico *Merluccius* are considered to be divergent forms of *M. albidus* (Karnella 1973). Several of the above authors have commented on the similarity in life history patterns of various species of *Merluccius*. Offshore hake, *M. albidus*, display some of these same patterns, indicating that aspects of their life histories are similar to those documented for other species.

Biological data concerning *M. albidus* are sparse. Those reported in this paper are limited primarily to the Gulf of Mexico. This study is a composite of published accounts, data acquired during resource assessment, gear evaluation and general exploratory cruises, and results of biological studies conducted by personnel of the Southeast Fisheries Center Pascagoula Laboratory, National Marine Fisheries Service (NMFS), NOAA.

MATERIAL AND METHODS

Specimens were collected with a variety of bottom trawls (Table 1) equipped with mud rollers, loop chain, floats, and usually a tickler chain. The larger trawls (38 to 60 m headrope) were fished with wooden bracket doors and ground cables whereas the smaller trawls (12 and 22 m headrope) utilized wooden chain doors. Mesh size on the larger trawls was 7.6 cm in the wings and body, 5.1 cm in the throat, and 4.5 cm in the cod end; smaller trawls had 5.1-cm mesh throughout with 3.8 cm in the cod end. In October 1971, a 22-m trawl with a 1.3-cm inner liner was used to collect juvenile *M. albidus*. Rough bottom areas were fished with a 12-m flat or semiballoon trawl and smooth areas with larger trawls (22 to 68 m).

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TABLE 1.—Trawling gear used by the RV *Oregon II* during slope fishery surveys in the Gulf of Mexico and Caribbean Sea from June 1969 through September 1973.

Trawl size (headrope length) (m)	(feet)	Door size (length × width) (m)	(feet)	Type of door
12	40	2.4 × 1.03	8 × 3.33	Wooden chain
22	71	3 × 1.12	10 × 3.67	Wooden chain
38	125	3 × 1.22	10 × 4	Iron bound wooden bracket
40	130	3 × 1.22	10 × 4	Iron bound wooden bracket
46	150	3 × 1.22	10 × 4	Iron bound wooden bracket
58	191	3 × 1.22	10 × 4	Iron bound wooden bracket
62	204	3 × 1.22	10 × 4	Iron bound wooden bracket
68	224	3 × 1.22	10 × 4	Iron bound wooden bracket

TABLE 2.—Gonad classification code — modified from Nikolsky (1963).

U-1	Gonads undeveloped, vestigial tubes, sex determination impossible by gross examination
Female:	
F-2	Immature gonads, sex determinable by gross examination, gonads very small, uninflated
F-3	Developing gonads, small yellow or white with no eggs visible to the naked eye
F-4	Maturing gonads, filled with opaque yellow to yellowish-orange eggs detectable by the naked eye
F-5	Ripe gonads, ovaries with translucent yellowish-white to whitish-green eggs easily expelled from the genital opening by lateral pressure on the gonads
F-6	Spent gonads, ovaries collapsed and bloodshot with some eggs being reabsorbed
Male:	
M-2	Immature gonads, sex determinable by gross examination, testes very small, uninflated
M-3	Developing gonads, inflated to the same degree as those of F-3 females and white or whitish-pink in color
M-4	Maturing gonads, inflated to same degree as those of F-4 females and milky white without free running milt
M-5	Ripe gonads, fully developed with free running white milt
M-6	Spent gonads, collapsed and bloodshot

Specimens were measured at sea to the nearest millimeter standard length (SL). Additional specimens were frozen for processing ashore, and were measured in standard, fork, and total lengths (SL, FL, and TL) for computation of a conversion curve and were also processed for length-weight relationship, gonad maturation, and stomach content data. Gonad maturation stages were classified by a scheme modified from that by Nikolsky (1963) and are listed in Table 2. Ovaries were weighed to the nearest 0.1 g. Otoliths removed from selected specimens (one specimen per centimeter SL) were prepared and evaluated following Jensen (1965). Morphometric and meristic measurements were taken as defined by Ginsburg (1954).

Age-class lines were computed using techniques described by Harding (1949) and Cassie (1954) and compared with ages determined from length-frequency data.

Weights were recorded to the nearest ounce on specimens larger than 200 mm SL and to the nearest 0.1 g on smaller fish. The method of least squares using the log transformation of the general equation $W = aL^b$ was used to compute the length-weight equations for males, females, and sexes combined.

The sample design for RV *Oregon II* cruise 27 allowed for equal effort per stratum regardless of stratum size, because distributional patterns and abundance levels of *M. albidus* were undefined. The sample area (Figure 1) on the De Soto Canyon slope north of Tampa, Fla., was divided into four 90-m depth strata ranging from 370 to 730 m. Each stratum was then further subdivided into 2.5 × 15 nautical mile sample sites (12,874 hectares per site). The entire sampling area of 84 sites totaled 1,081,416 hectares. Five sample sites were randomly selected within each 90-m depth stratum from a number table; however, only four sites were sampled in stratum 4 due to a malfunction of the trawl. No special consideration in site selection was given to latitude.

Each sample site was fished with a 40-m trawl (Table 1) for 5 h at 3 knots with a 2.5:1 scope ratio (i.e., 2.5 m of wire out for each meter of depth). Drag distance was variable because of changes in the surface and bottom currents. Area swept in hectares per drag was computed by measuring the distance between the starting and ending point of each tow and multiplying by a conversion factor. An XBT (expendable bathythermograph) probe was dropped at the start and finish of each station.

Standing stock estimates were computed using an "area-swept" method. This method is computed as follows:

$$SS_i = (\bar{P}_{wi})(A_i) \quad (1)$$

where SS_i = standing stock estimate in the ith area

$\bar{P}_{wi}$ = average population expressed as kilograms per hectare in the ith area

A_i = total bottom area within the ith area.

$$SS_{tot} = \sum_{i=1}^{4} SS_i$$

where SS_{tot} = total standing stock estimate expressed as kilograms

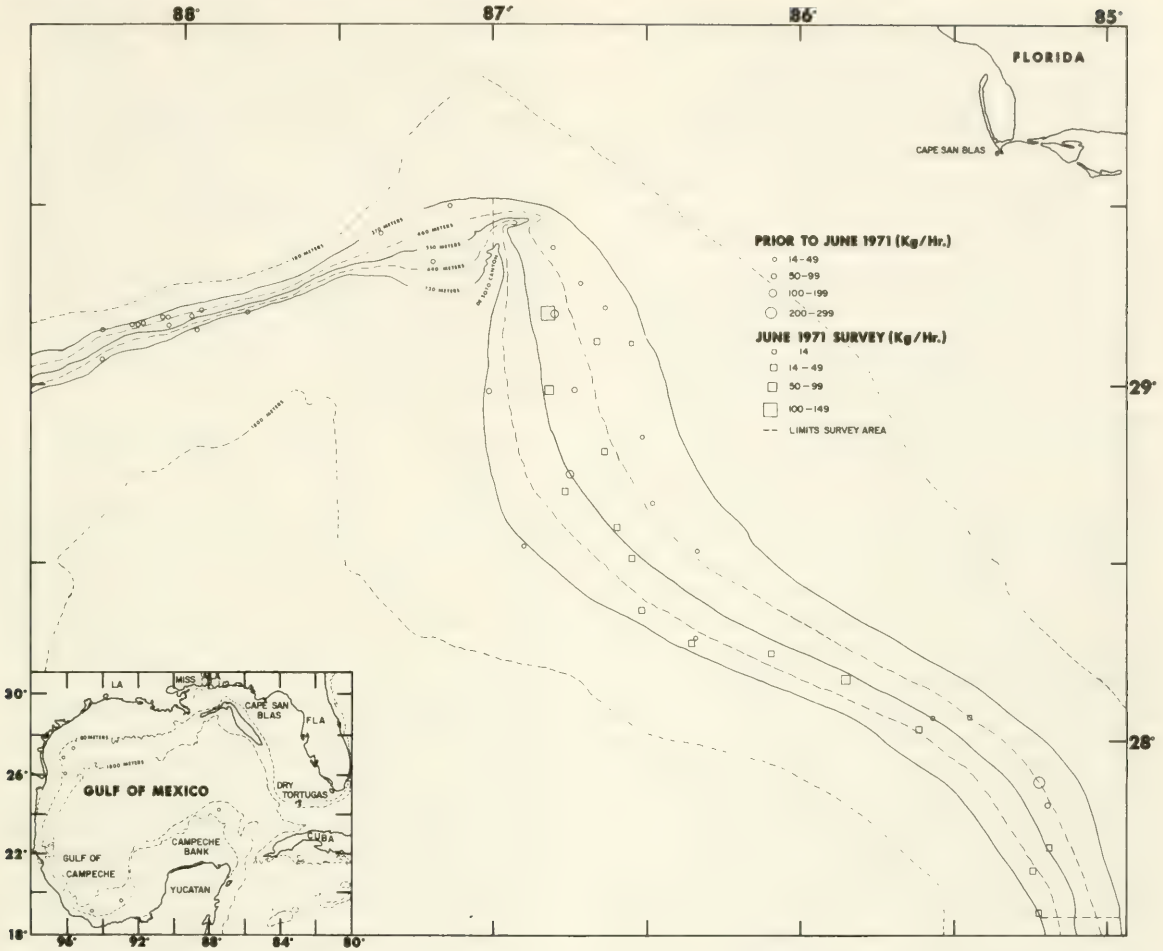

FIGURE 1.—Northeastern section of the Gulf of Mexico showing stations on De Soto Canyon slope north of Tampa, Fla., made during the June 1971 finfish survey and the Mississippi Delta slope; insert of entire Gulf of Mexico identifying all stations between 1950 and 1971 where the catch rate of *Merluccius albidus* exceeded 14 kg/h.

SS_i = the computed standing stock estimates for each area.

Confidence intervals were calculated using the weighted pooled variance method described by Snedecor and Cochran (1967):

$$S_{\bar{x}_{tot}} \sqrt{w_i^2 \, s_i^2/n_i} \qquad (2)$$

where $S_{\bar{x}_{tot}}$ = standard error of the mean
$\bar{x}_{tot}$ = mean density (kilograms/hectare) weighted by area
w_i = weighting factor based on sample size, i.e., $w_i = n_i/N$
s_i^2 = variance of density estimate for ith stratum.

The weighted pooled variance was used to reduce the variation associated with different sample sizes within each stratum.

DISTRIBUTION AND ABUNDANCE

The range of *M. albidus* in the western Atlantic extends from lat. 41°N off Georges Bank (Bigelow and Schroeder 1955) to the Orinoco Delta and possibly to the vicinity of Rio de Janeiro (Cervigon 1966). Bigelow and Schroeder (1955) reported a depth range of 92 to 1,170 m for *M. albidus* on the New England slope with approximately 75% of the population residing in depths of 185 to 550 m. *Merluccius albidus* are seldom caught by commercial hake fishermen in New England (Fritz

1960), suggesting a low population level, unavailability to the fleet, or lack of recognition by the fishermen. However, mixed commercial concentrations of *M. albidus* and *M. bilinearis* were found south of Hudson Canyon on the edge of the shelf by the RV *Albatross III* (Edwards et al. 1962) and on Georges Bank by West German stern trawlers (Mombeck 1971).

Exploratory fishing data from the Pascagoula data files showed that *M. albidus* composed 25% of the total finfish available to trawl gear between 350 and 1,000 m on the Mississippi slope and 60% between 450 and 730 m on the west Florida-De Soto Canyon slope. Several large catches containing individual fish weighing in excess of 0.45 kg have been made by NMFS vessels.

In the Gulf of Mexico, *M. albidus* have been taken at depths of 142 to 1,100 m. Between 1950 and 1971, NMFS vessels caught *M. albidus* at 73% of all trawl stations in depths of 182 to 1,100 m.

Relative apparent abundance of *M. albidus* in the Gulf of Mexico was established by computing catch rates based on historical fishing records. Highest concentrations occurred in the northern Gulf between Tampa, Fla., and the Mississippi Delta. Prior to the *M. albidus* assessment cruise in June 1971, catch rates of 14 kg/h (31 pounds/h) or greater occurred at only 37 Gulf of Mexico stations (Figure 1) of which 78% had catch rates less than 50 kg/h. These stations are primarily in the northeast quadrant of the Gulf of Mexico in depths of 370 to 930 m (Figure 1). Maximum catch rates recorded for this period in the Gulf of Mexico are as follows: north Gulf, De Soto Canyon, 640 m, 161 kg/h; east Gulf, off Tampa, 490 m, 284 kg/h; west Gulf, east of Brownsville, Tex., 430 m, 31 kg/h; south Gulf, east of Veracruz, Mexico, 540 m, 22 kg/h; and north of Campeche Bank, 550 m, 20 kg/h.

Nineteen 5-h trawling stations were completed on the De Soto Canyon slope in June 1971 to obtain biological data and estimate the size of the *M. albidus* population. Catch rates varied from 5.7 to 144.0 kg/h in depths of 370 to 730 m and averaged 38.7 kg/h (Figure 1).

Highest catch rates of *M. albidus* after June 1971 were 12.5 kg/h in 440 m on the western slope of De Soto Canyon, 15.5 kg/h in 550 m south of Dry Tortugas, and 58.5 kg/h in 420 m on the De Soto Canyon east slope. These catch rates may be artificially low, as the trawls used were not rigged specifically for catching *M. albidus*. Abundance in the western and southern Gulf of Mexico is unknown due to the considerable area of untrawlable bottom off Texas, western Louisiana, and in the Gulf of Campeche.

Merluccius albidus were caught at depths of 200 to 795 m in the Caribbean Sea including the insular slopes of the Antilles. During a 1970 trawl survey on the Caribbean slope between Belize and Aruba, it was taken most frequently at depths of 450 to 630 m north of Aruba. Caribbean trawling records give no indication of any significant concentrations of *M. albidus*. However, Cervigon (1964) reported that *M. albidus* may be of economic importance off Venezuela in depths greater than 370 m.

RELATION OF DEPTH TO SIZE AND SEX

Studies have shown that size increases with bottom depth in various species of hake (Grinols and Tillman 1970). Rohr (1972) showed that *M. albidus* segregates by size and sex on the continental slope in the Gulf of Mexico (Figures 2, 3). Juveniles of both sexes, young adult females, and adult males inhabit the upper slope (depths <550 m) while larger, mature females are concentrated on the lower slope (depths >550 m). This pattern is clearly demonstrated when plotting the male-female ratio vs. depth (Figure 3).

A similar distributional pattern of *M. albidus* was reported on the Honduran-Panamanian slope by Bullis and Struhsaker (1970) and observed by the senior author on both the western and southern Caribbean slopes from Belize to Aruba.

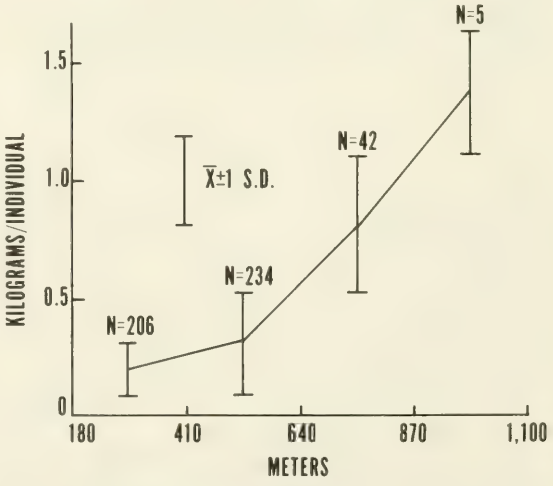

FIGURE 2.—Average weight of individual *Merluccius albidus* vs. depth for 487 trawl stations in the Gulf of Mexico.

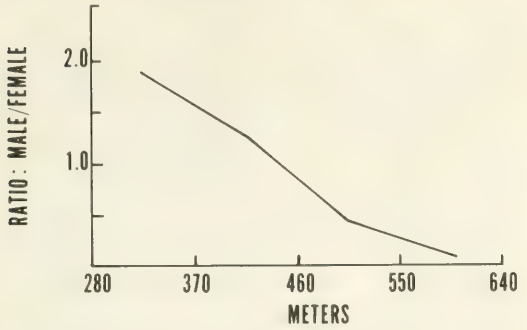

FIGURE 3.—Ratio of male to female *Merluccius albidus* decreases with increasing depth.

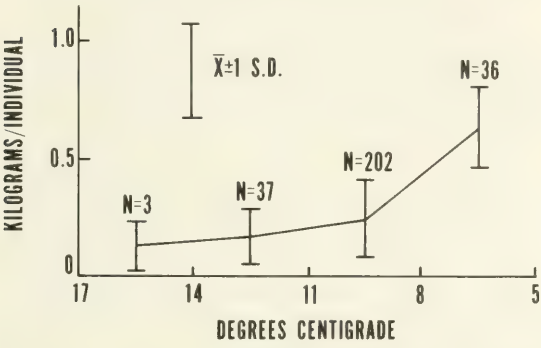

FIGURE 4.—Average weight of individual *Merluccius albidus* vs. bottom temperature for 278 trawl stations in the Gulf of Mexico.

An increase in size of *M. albidus* with increasing depths and decreasing temperature was observed in the present study (Figures 2, 4; Table 3).

REPRODUCTION

Fecundity data of *M. albidus* were not collected; however, a partially spent 680-mm SL female taken on the De Soto Canyon slope in August 1970 yielded an estimated 340,000 greenish-white eggs weighing 340 g. Advanced eggs in the ovaries of *M. productus* ranged from 80,000 in small, 350 mm SL, to 496,000 in large, 690 mm SL, specimens (MacGregor 1966). Since the estimated number of eggs in the specimen of *M. albidus* is somewhat similar to that of *M. productus*, the fecundity of the two species may be similar.

A spawning period extending from late spring to early autumn is hypothesized for *M. albidus* in the Gulf of Mexico and Caribbean Sea. Ripe fish were observed as early as May and as late as October. Running ripe males and females were taken together in September 1973 on the Mississippi Delta and De Soto Canyon slope (Table 4). Females caught in February were in an advanced resting stage, i.e., gonad maturation stage 4. Spawning occurs in New England from April to July (Colton and Marak[3]). Some species of *Merluccius* spawn throughout much of the year, although most have a short spawning period varying in time for individual species (Grinols and Tillman 1970).

Gonad maturation data suggest that spawning occurs near the bottom in depths of 330 to 550 m. Limited numbers of ripe fish were taken during cruises which surveyed both the upper and lower

[3]Colton, J. B., Jr., and R. R. Marak. 1969. Guide for identifying the common planktonic fish eggs and larvae of continental shelf waters, Cape Sable to Block Island. Biol. Lab., Woods Hole, Mass. Lab. Ref. 69-9, 15 Sept. 1969.

TABLE 4.—Date, area, and depth at which ripe *Merluccius albidus* have been collected in the Gulf of Mexico.

Date	Area	Depth (m)
	Females	
June 1970	Gulf of Campeche	360-730
Aug. 1974	Central north Campeche Bank slope	570-550
Aug., Sept. 1970	De Soto Canyon	380-770
June 1971	East De Soto Canyon and west Florida slope	370-730
Oct. 1971	East Mississippi Delta slope and west De Soto Canyon slope	550-730
May 1973	Mississippi Delta-west De Soto Canyon slope	460
May 1973	Dry Tortugas slope	372
Sept. 1973	Mississippi Delta-west De Soto Canyon slope	330-460
	Males	
Aug. 1970	Dry Tortugas slope	550
Aug. 1970	West Florida slope off Tampa, Fla.	275
Aug. 1970	East De Soto Canyon slope	390
May 1973	Mississippi Delta-west De Soto Canyon slope	357
May 1973	Dry Tortugas slope	350-550
Sept. 1973	Mississippi Delta-west De Soto Canyon slope	330-460

TABLE 3.—Range and mean fishing depths, bottom temperatures, lengths, and weights of *Merluccius albidus* sampled on the De Soto Canyon slope north of Tampa, Fla., in June 1971.

Stratum	Depth (m)		Temperature (°C)		Number fish sampled	Standard length (mm)		Weight (g)	
	Range	X̄	Range	X̄		Range	X̄	Range	X̄
1	370-459	409	9.3-11.0	10.1	497	47-455	234	1- 985	158
2	460-549	500	7.8- 9.6	8.3	494	215-520	299	42-1,550	360
3	550-639	577	5.6- 8.5	6.9	488	268-562	389	265-1,960	624
4	640-730	686	5.6- 6.7	6.3	392	313-575	424	315-2,070	818

slopes. Ripe males were not found at depths greater than 550 m (Figures 5, 6, 7). Since few ripe fish were caught by bottom trawls, it is possible that spawning occurs at some distance above the bottom. First time spawners appear to move down slope to spawn whereas the older maturing females (spawning for their second or more times) were found lower on the slope and moved up the slope into the spawning area.

Few spent males or females were taken during this study. Spent females may move down the slope from the spawning area to recover and then gradually move back up the slope to enter a resting stage. Alternatively, after spawning they might immediately move onto the upper slope in depths of 180 to 360 m to feed and recover, and finally move back into depths greater than 360 m to enter the resting stage.

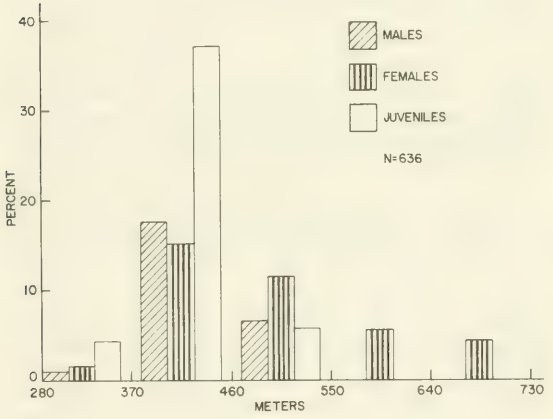

FIGURE 5.—Distribution of male, female, and juvenile *Merluccius albidus* by depth on the east Mississippi Delta and west De Soto Canyon slope in October 1971.

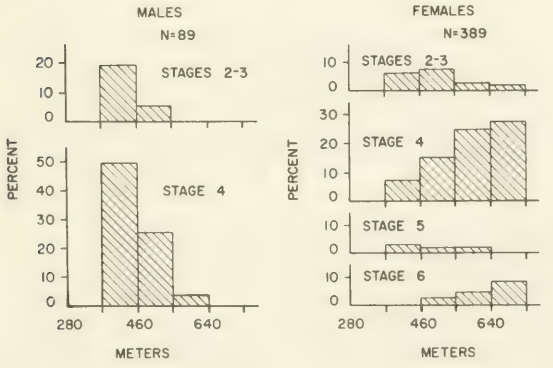

FIGURE 6.—Gonad maturation stages of *Merluccius albidus* by depth on the west Florida-De Soto Canyon slope in June 1971.

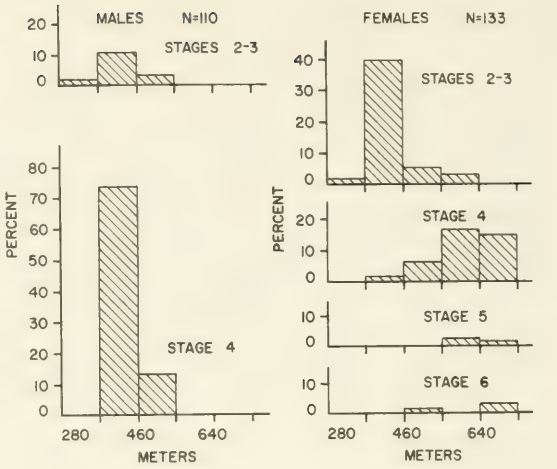

FIGURE 7.—Gonad maturation stages of *Merluccius albidus* by depth on the east Mississippi Delta and west De Soto Canyon slopes in October 1971.

European, Argentinean, and Pacific hake are reported to feed ravenously after spawning. If *M. albidus* follows this pattern, it would probably move up to the shelf edge following spawning, as a richer supply of food is available in this area. Additional deepwater samples are needed before this hypothesis can be tested.

Spawning males and females were found together at depths of 330 to 460 m but only one spent male and female were caught in the same tow.

Merluccius albidus may spawn later in the Caribbean than in the Gulf of Mexico. In November 1970, 11 of 21 females collected off Aruba in 604 m were in spawning condition. Spent females were also found in November 1970 in depths of 550 to 730 m off Colombia. The depth distribution of females in the Caribbean appears to be similar to that in the Gulf of Mexico; but data are very limited. Only one male was collected from the Caribbean.

Merluccius albidus are also distributed on the slope in relation to gonad maturation stages. Eighty-eight percent of the juveniles occurred in 370 to 460 m. They were observed at other times and at other geographic sites in the Gulf of Mexico and Caribbean Sea, but always on the upper slope between 180 and 460 m. It is possible that the distribution of juveniles seen in October is similar to their overall distributional pattern.

The distribution of gonad stages of male and female *M. albidus* on the Mississippi Delta and De Soto Canyon slopes in 1971 are shown in Figures 6 and 7. Males were found primarily on the upper

slope (280 to 550 m) during both June and October. Only 1.3% of all males taken were caught in depths exceeding 550 m, with 613 m being the maximum depth at which males were taken. Females were found throughout the depth ranges surveyed (Figures 5, 6, 7).

Location of *M. albidus* on the slope appeared to be dependent on gonad maturation stage and size of individuals. In 1971, stage 4 males dominated at all depths where males were collected except in 280 to 370 m; neither ripe (stage 5) nor spent (stage 6) males were taken (Figures 6, 7). In 1973, the data showed a predominance of stage 4 males though a few ripe and spent males were found (Table 5). Males, regardless of maturation stage, were always taken in depths less than 550 m. The predominance of stage 4 male *M. albidus* in the autumn of 1971 and 1973 (Figure 7, Table 5) suggests that stage 4 is an advanced resting stage, with these fish not spawning until the following spring. The stage 4 males were probably in the spawning cycle in the spring of 1971 and 1973 (Figure 6, Table 5) and would have spawned some time during the summer based on a spring-summer spawning period for *M. albidus*.

Female *M. albidus* of all sizes and maturation stages were found throughout the depth range surveyed. Young females mixed with males and juveniles on the upper slope, but larger females predominated on the lower slope. Lower slope females, larger than 250 mm SL, caught in the autumn were in the gonad resting stage and would not spawn until spring or summer. Females in stages 2-4 were most frequently caught as they were in the prespawning and/or resting stages. The paucity of ripe or spent females caught in trawls is evident from Figures 6 and 7 and Table 5. The few ripe and spent females (stages 5, 6) caught in 1973 (Table 5) were partially a result of the depths at which fishing operations were conducted, as few stations exceeded 600 m. Ripe and spent female *M. albidus* were found lower on the slope than were stages 2-4.

Eggs and early larval stages (first 84 h) of *M. albidus* off Martha's Vineyard (New England) were described by Marak (1967), but larvae larger than 4 mm SL are unreported. Egg and early larval development of *M. albidus* in the Gulf of Mexico and the tropical Atlantic may be similar to that off New England, although hatching may be more rapid in warmer latitudes than the 6 to 8 days reported by Marak (1967). Larvae reared by Marak (1967) ranged in length at hatching from 3.05 to 3.75 mm, averaging 3.5 mm and were relatively undeveloped. The yolk was small and was rapidly assimilated after hatching, thereby necessitating early initiation of feeding.

FOOD HABITS

All hake species are opportunistic feeders (Grinols and Tillman 1970). In the Gulf of Mexico, *M. albidus* feed on a large variety of items found on and off the bottom (Table 6).

A feeding pattern based on adaptive zones of prey species (i.e., epipelagic, mesopelagic, and benthic) suggests that hake feed primarily on benthic and mesopelagic organisms (Table 7). The lack of a day-night differential in bottom trawl catch rates (Table 8) suggests that *M. albidus* feed on or near the bottom since a differential would be expected if *M. albidus* moved well off the bottom to feed.

Merluccius albidus apparently feed at about the same rate throughout the day except near dawn (0500-0700, Table 9). The higher incidence of food in the stomach during daylight hours corresponds to the time when the mesopelagic fauna are closer to the bottom. This hypothesis is reinforced as 81% of the myctophids were found in stomachs from fish caught during daylight hours (0700-1800), and in only 1% of the stomachs from fish caught at dusk (1800-2000). The mesopelagic fauna leaves the bottom at dusk and moves higher in the water column, thus becoming unavailable as prey to the hake. Stomachs from specimens caught at night

TABLE 5.—Maturation stages in Gulf of Mexico *Merluccius albidus* for May and September 1973 listed as percentage of occurrence.

	May				September	
	Mississippi Delta-west De Soto Canyon slope 344-730 m		Dry Tortugas slope 353-595 m		Mississippi Delta-west De Soto Canyon slope 330-503 m	
Gonad state	Females N = 1,069	Males N = 59	Females N = 323	Males N = 525	Females N = 2,083	Males N = 1,430
2-3	43.3	6.8	96.6	6.5	65.3	7.2
4	55.7	88.1	2.2	66.1	32.5	79.0
5	0.4	5.1	1.2	20.4	1.6	12.1
6	0.6	0.0	0.0	7.0	0.6	1.7
Total	100.0	100.0	100.0	100.0	100.0	100.0

TABLE 6.—General systematic list of prey species identified from the stomachs of 649 *Merluccius albidus*. List is arranged alphabetically.

FISHES
- Apogonidae
  - *Epigonus pandionus*
  - *Synagrops* sp.
  - *Synagrops bella*
  - *Synagrops spinosa*
- Argentinidae
  - *Argentina striata*
- Ariommidae
  - *Ariomma* sp.
  - *Ariomma bondi*
- Bathyclupeidae
  - *Bathyclupea* sp.
- Brotulidae
  - *Dicrolene intronigra*
  - *Monomitopus agassizi*
- Carangidae
  - *Trachurus lathami*
- Chauliodontidae
  - *Chauliodus sloani*
- Chlorophthalmidae
  - *Chlorophthalmus agassizi*
- Clupeidae
  - *Etrumeus teres*
- Evermanellidae
  - *Evermanella* sp.
- Gempylidae
  - *Nesiarchus nasustus*
  - *Scombrolabrax heterolepis*
- Gonostomatidae
  - *Gonostoma* sp.
  - *Gonostoma elongatum*
  - *Maurolucius mulleri*
  - *Polymetme corythaeola*
  - *Triplophos hemingi*
  - *Yarella blackfordi*
- Macrouridae
  - *Bathygadus macrops*
  - *Coelorhynchus carminatus*
  - *Coryphaenoides colon*
  - *Gadomus arcuatus*
  - *Gadomus longifilis*
  - *Hymenocephalus italicus*
  - *Malacocephalus* sp.
  - *Nezumia* sp.
  - *Nezumia aequalis*
- Malacosteidae
- Melanostomatidae
- Merlucciidae
  - *Merluccius albidus*
  - *Steindachneria argentea*
- Myctophidae
  - *Lampadena luminosa*
  - *Neoscopelus macrolepidotus*
- Nomeidae
  - *Cubiceps* sp.
  - *Psenes* sp.
- Percophididae
  - *Bembrops* sp.
  - *Bembrops gobioides*
- Polymixiidae
  - *Polymixia lowei*
- Squalidae
  - *Etmopterus schultzi*
- Sternoptychidae
- Stomiatidae
- Trichiuridae
- Unidentified fishes

MOLLUSKS
- Limpets
  - Fissularidae
- Squids
  - *Illex* sp.
  - *Illex illecebrosus*
  - *Oregoniateuthis springeri*
  - *Pholidotheuthis adami*
- Unidentified squids

CRUSTACEANS
- Caridea
- Euphausiacea
- Euryonidae
  - *Steromastis sculpta*
- Glyphocrangonidae
  - *Glyphocrangon* sp.
  - *Glyphocrangon alispina*
- Nematocarcinidae
  - *Nematocarcinus* sp.
- Oplophridae
  - *Notostomus* sp.
- Pandalidae
  - *Plesionika acanthonotus*
- Pasiphaeidae
  - *Pasiphaea* sp.
- Penaeidae
  - *Aristeus antillensis*
  - *Benthysicymus* sp.
  - *Hymenopenaeus* sp.
  - *Hymenopenaeus debilis*
  - *Hymenopenaeus robustus*
  - *Parapenaeus* sp.
  - *Penaeopsis megalops*
- Unidentified crustaceans
- Unidentified shrimps

UROCHORDATA
- Pyrosomidae
  - *Pyrosoma* sp.

TABLE 7.—Types of identified prey, according to the adaptive life zone they inhabit, from the stomachs of 649 *Merluccius albidus*.

Adaptive zone	Taxa	Frequency	Percent total frequency
Epipelagic	Carangidae and Clupeidae	7	1.4
Subtotal		7	1.4
Mesopelagic	Myctophidae	84	16.5
	Miscellaneous fishes	20	3.9
	Squids	95	18.7
	Euphausiacea	10	2.0
	Miscellaneous crustacea	4	0.8
	Pyrosomidae	1	0.2
Subtotal		214	42.1
Benthic	*Steindachneria argentea*	142	28.0
	Apogonidae	21	4.1
	Ariommidae	17	3.3
	Macrouridae	17	3.3
	Merluccius albidus	12	2.4
	Trichiuridae	11	2.2
	Miscellaneous fishes	30	5.9
	Penaeopsis megalops	21	4.1
	Penaeidae	7	1.4
	Miscellaneous crustaceans	7	1.4
	Mollusks	2	0.4
Subtotal		287	56.5
Grand total		508	100.0

TABLE 8.—Catch rates of *Merluccius albidus* and trawl effort by time of day on the slope in the Gulf of Mexico during May 1973.

Item	Day 0700-1759	Twilight 0500-0659 1800-1959	Night 2000-0459
Average no. of fish/hour	15.2	13.6	14.5
Hours fished	60.75	34.00	54.00

TABLE 9.—Frequency of *Merluccius albidus* stomachs containing food, from the Gulf of Mexico in 330 to 730 m during May and September 1973, in 4-h intervals.

Time of day	No. fish sampled	Number stomachs containing food	Percent frequency stomachs with food
0000-0300	566	56	9.9
0400-0700	1,121	61	5.4
0800-1100	679	84	12.4
1200-1500	724	64	8.8
1600-1900	963	117	12.1
2000-2300	1,315	131	10.0
Total	5,368	513	9.6

contained primarily members of the resident benthic community.

This feeding behavior is in contrast to that described for other species of *Merluccius*. Initiation of feeding after sunset has been suggested for *M. productus* (Alton and Nelson 1970) and for all hake (Hickling 1927).

Most offshore hake caught during the survey regurgitated due to changes in hydrostatic pressure with only 8.2% (651 of 7,944) of those stomachs examined containing food. Fishes composed the major portion of the diet of *M. albidus*, followed by squid and crustaceans (Table 7). Fishes were exclusively present in about 75% of the stomachs examined and either singularly or together with crustaceans and squid in about 80% of these stomachs. Twenty-nine percent of the fishes eaten were mesopelagic and 69% were benthic.

Thirty-two identifiable prey species from *M. albidus* stomachs are listed in Table 6 by familial groups. *Steindachneria argentea* (Merlucciidae) was found most frequently, followed by species of Myctophidae (Table 7). About 2% of the specimens examined had been feeding on juvenile *M. albidus* indicating some degree of cannibalism.

Benthic penaeid and caridean shrimp were the dominant crustaceans found in stomachs of *M. albidus*. *Penaeopsis megalops* was the dominant

penaeid shrimp and suggests selective feeding by *M. albidus*. Stomachs of *M. albidus* contained a higher frequency of *P. megalops* than *Hymenopenaeus robustus* even at those stations where *H. robustus* was more abundant. Abundance of these two species was based on the catch rates when they were taken together. This preference may indicate a feeding migration to depths of greater abundance of *P. megalops*.

Merluccius albidus are active predators with type and size of prey varying as follows: juveniles (90 to 149 mm SL) contained primarily shrimp 29 to 45 mm TL with a few fragments of fishes and squid; maturing adults (150 to 299 mm SL) contained a variety of fishes 100 to 240 mm TL, with one 320-mm TL trichiurid, crustaceans 40 to 130 mm TL, and squid 38 to 160 mm ML (mantle length); adults (larger than 300 mm SL) contained primarily Stomiatoidei fishes 100 to 240 mm TL, macrourids 150 to 255 mm TL, trichiurids up to 500 mm TL, caridean shrimp 49 to 80 mm TL, and squid 70 to 170 mm ML.

AGE AND GROWTH

Otoliths have been used successfully to estimate ages of several species of *Merluccius*. Annual growth patterns for *M. productus* were defined and used to establish age composition (Nelson and Larkins 1970). Botha (1969) used otoliths to establish the growth rates of both *M. capensis* and *M. paradoxus* and concluded that zonation and composition of the otoliths from various species of *Merluccius* were similar.

Otoliths of *M. albidus* have well-defined opaque and hyaline zones which increase in number with size and age of the fish. However, an analysis of the complex banding pattern in 206 pairs of otoliths from juveniles (7 to 14 cm TL) was impossible, because all bands were not defined and slow growth rings (hyaline bands) did not agree with age estimates based on length frequencies. Similar difficulties were encountered in the analysis of otoliths from 56 males (15 to 34 cm TL) and 171 females (15 to 54 cm TL).

The tentative age structure presented for Gulf of Mexico *M. albidus* was based on length frequency data (Figure 8, Table 10). Harding-Cassie age-class lines were computed (Harding 1949; Cassie 1954) based on the lengths of 1,839 males and 2,852 females taken in October 1971 and September 1973. Calculated mean lengths were very similar to those shown on Table 10 for both male

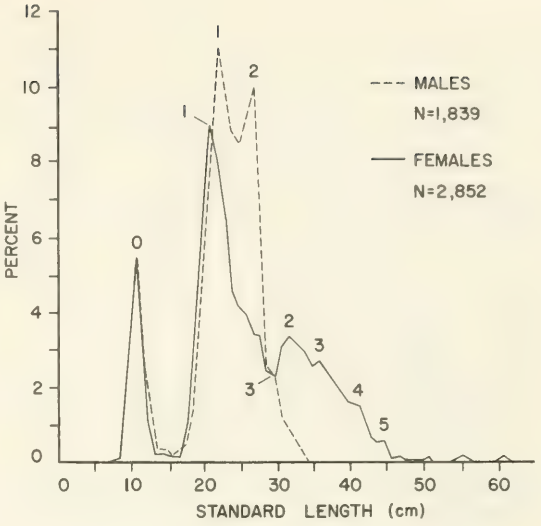

FIGURE 8.—Length frequency and modal size for ages 0 to 5 for *Merluccius albidus* from the east Mississippi Delta and west De Soto Canyon slope October 1971 and September 1973.

TABLE 10.—Tentative ages with midpoint of modal size groups of northern Gulf of Mexico *Merluccius albidus*.

	Males		Females	
Age (yr)	SL	TL	SL	TL
0	10.5	11.8	10.5	11.8
1	21.5	24.0	20.5	22.9
2	26.5	29.6	31.5	34.1
3	29.5	32.9	36.5	40.6
4			40.5	45.1
5			44.5	49.5

and female *M. albidus*. Longevity of *M. albidus* is unknown, but Botha (1971) reported that Cape hake live at least 11 yr. Juvenile male and female *M. albidus* are about the same size, but males are slightly larger than females at age 1. However, females are significantly larger by age 2 with difference becoming more evident as the fish becomes older (Figures 8, 9; Table 10). The largest male caught during this study was 404 mm SL and 0.6 kg while the largest female was 680 mm SL and 4.1 kg. The growth rate until age 1 was similar in both sexes. Thereafter, males which mature earlier use a proportion of their available energy to produce sexual products which may result in their reduced growth and smaller size. Because females mature later, they direct more of their energy toward growth for a longer period of time resulting in their larger size.

Female *M. albidus* between ages 4 and 5 grow at a rate about equal to that reported for female *M. productus* (Nelson and Larkins 1970; Table 11).

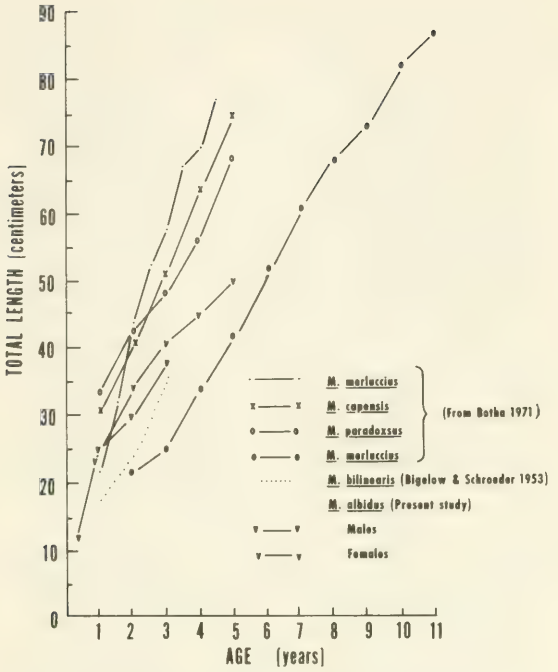

FIGURE 9.—Comparative growth rates for five species of Atlantic *Merluccius: M. merluccius, M. capensis,* and *M. paradoxus* from various authors after Botha (1971, fig. 17), *M. bilinearis* from Bigelow and Schroeder (1953), and *M. albidus* (present study).

TABLE 11.—Comparative length in centimeters by age for *Merluccius albidus, M. capensis, M. paradoxus,* and *M. productus*.

Age	TL *M. albidus*[1]		TL *M. capensis*[2]		TL *M. paradoxus*[2]		FL *M. productus*[3]	
(yr)	Male	Female	Male	Female	Male	Female	Male	Female
2	29.6	34.1						
3	32.9	40.6	27.6	31.0	31.3	32.6		
4		45.1	38.1	40.0	39.4	41.7	46.5	45.7
5		49.5	47.3	48.5	45.4	49.8	49.5	50.8
6			55.3	56.5	49.7	57.3	52.8	53.9
7			62.1	63.9	52.9	63.3	54.4	56.4
8			68.0	70.9		68.9	55.4	58.7
9			73.1	77.5		73.9	56.1	59.7
10			77.5	83.6		78.3	56.6	60.7
11			81.4	89.3		82.2		61.2
12								61.5

[1]Data from Table 10 of present study.
[2]Calculated lengths from Botha (1971).
[3]Calculated lengths (Nelson and Larkins 1970); Dark (1975) gives similar calculated lengths for *M. productus* including estimates for 1, 2, and 3 yr fish as 16.6, 26.2, and 41.1 FL.

Growth rates of male and female *M. productus* (Dark 1975) indicate that growth is rapid during the first 3 yr but then slows perceptibly. Gulf of Mexico *M. albidus* are larger than *M. productus* at age 2. However, the growth rates of 3- to 5-yr-old female *M. albidus* and *M. productus* appear similar. Growth rates of males of these species do not appear to be similar. *Merluccius albidus* from the Gulf of Mexico appear to grow faster than *M. bilinearis* (Figure 9).

A small number of female *M. albidus* were collected in February 1970 below the head of De Soto Canyon in depths of 550 to 730 m. These fish ranged from 21 to 59 cm SL and showed modal peaks at 36, 40, and 44 cm SL which were similar to the peaks shown in Figure 8. Females collected on the De Soto Canyon slope in June 1971 at depths of 550 to 730 m showed modal peaks at 38, 42, and 45 cm SL.

Length frequency data imply that males rarely live longer than 3 yr whereas a large number of females live at least 5 yr (Figures 8, 9; Tables 10, 11). However, longevity in other species of *Merluccius* is reported as upwards of 13 yr for females and 11 yr for males. Additional sampling lower on the slope throughout the year may generate a broader data base from which additional age-classes could be defined bringing longevity of *M. albidus* in closer agreement to other species of *Merluccius*. Figure 8 suggests a high mortality rate for 2- to 3-yr-old males residing higher on the slope which probably increases their accessibility to predators. Botha (1971) showed that male *M. paradoxus* do not live as long as females and stated that males over 7 yr of age are extremely rare.

A length-weight curve for males and females was computed from 1,920 specimens from the Gulf of Mexico (Figure 10). Rate of weight increase was similar in both sexes up to about 18 cm SL, after which the rate of increase for males became greater possibly because males develop mature gonads earlier.

STANDING STOCK OF *M. ALBIDUS* IN THE GULF OF MEXICO

The standing stock estimate and confidence interval for each stratum and for all strata are listed in Table 12. Maximum density per drag in June 1971 was 11 kg/hectare, mean density 3 kg/hectare, and minimum density 0.45 kg/hectare.

Since trawl efficiency or catchability coefficient (q) is unknown for offshore hake, a q of 1 was used in the calculations thereby minimizing the standing stock estimate. Catchability of any trawl is somewhat dependent on several biological, physiological, and adaptive characteristics of the species sought which must be considered in assigning a value to q. Other species of hake come off the bottom to feed and *M. productus* forms large schools about 9 m off the bottom (Nelson and

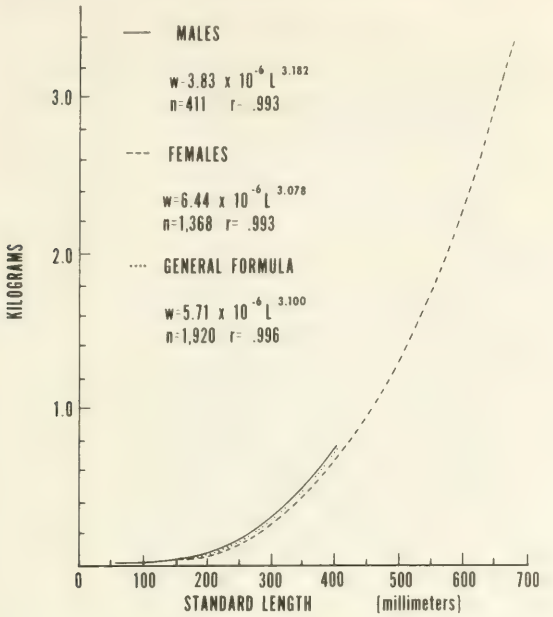

FIGURE 10.—Length-weight relationship of *Merluccius albidus* from the Gulf of Mexico.

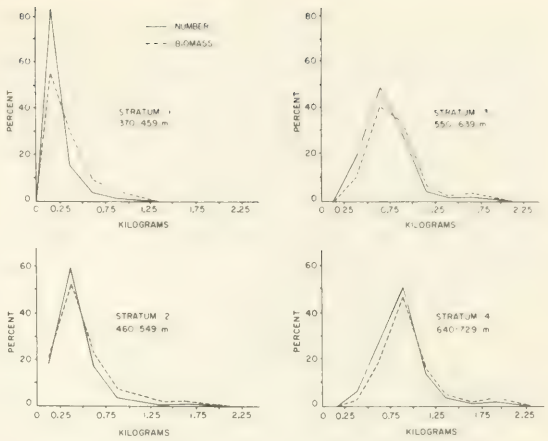

FIGURE 11.—Number and biomass of *Merluccius albidus* by 90-m depth strata on De Soto Canyon slope north of Tampa, Fla., June 1971.

Larkins 1970). If such behavior is characteristic of *M. albidus,* then it may be necessary to use both mid-water trawls and higher-opening fish trawls, coupled with more tows of a shorter duration. More short tows will allow greater coverage of the grounds and dampen inherent variability in the catch rates. This will enable us to develop more realistic population estimates.

Distribution and abundance of *M. albidus* on the De Soto Canyon grounds north of Tampa show that the largest segment of the stock was located in stratum 2 (Figure 11, Table 12). Numbers of fish were highest in stratum 1 (49%) but they only represented 22% of the population biomass. Most commercial-sized (greater than 0.45 kg) *M. albidus* were caught in strata 3 and 4 (Figure 11).

Commercial potential for this species is considered to be low, particularly when compared to landings of presently exploited hake species. Landings of various species of *Merluccius* in 1965 were in excess of 9.1×10^9 kg (Grinols and Tillman 1970) yet our standing stock estimate is only slightly more than 3.4×10^6 kg and our highest recorded catch was only 284 kg/h.

Additional effort must be expended in order to classify the life history and to test the hypothesis discussed in this paper. Population estimates must be more realistic and delineation of the grounds occupied by this species more precise. *Merluccius albidus* are known to occur from Georges Bank to off the northeastern coast of South America; however, presently little is known concerning its population, life history, or commercial potential.

ACKNOWLEDGMENTS

Richard B. Roe, NMFS, NOAA, Wash., D.C., assisted in developing the computer program to calculate the length-weight equations. D. Nolf, Rijksuniversiteit Gent, Belgium, supplied the

TABLE 12.—Standing stock estimates of both weights and numbers for *Merluccius albidus* on the De Soto Canyon slope north of Tampa, Fla.; estimates are based on 19 5-h tows made in June 1971 using a 40-m fish trawl with 3-m bracket doors.

Stratum number	Depth (m)	Area (hectares)	Number of samples	Area sampled (hectares)	Total catch (kg)	Mean density[1]	Biomass (kg × 10^6)	Percent biomass	Biomass estimate[2] (kg × 10^6)	Number of individuals × 10^5	Percent individuals
1	370-459	327,410	5	326.2	716	2.19	0.72	22	0.26-1.20	5.27	49
2	460-549	310,400	5	318.2	1,424	4.48	1.39	42	0-2.87	3.70	34
3	550-639	247,618	5	294.0	883	3.00	0.75	23	0.51-0.99	1.21	11
4	640-730	195,788	4	253.6	576	2.27	0.44	13	0.27-0.63	0.61	6
Total		1,081,216	19	1,192.0	3,599	3.02	3.30	100	2.15-4.47	10.79	100

[1]Values in kilograms per hectare.
[2]Confidence interval = 90%.

samples of eastern Atlantic *M. merluccius* otoliths, examined the Gulf of Mexico *M. albidus* otoliths, and provided copies of his plates of otoliths of both Atlantic and Pacific species of *Merluccius* (unpublished monograph on Gadidae otoliths). David M. Cupka, South Carolina Wildlife and Marine Resource Department, Charleston, S.C., kindly identified the squids commonly found in *M. albidus* stomachs. D. M. Cohen kindly reviewed the manuscript.

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BEHAVIOR OF CALIFORNIA GRAY WHALE, *ESCHRICHTIUS ROBUSTUS*, IN SOUTHERN BAJA CALIFORNIA, MEXICO

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ABSTRACT

Mother-young pairs of the California gray whale, *Eschrichtius robustus*, have been studied by a variety of means, including direct observation in calving lagoons from shore and ship, from aircraft, and by attachment of jettisonable instrument packages to calves. Instrumented whale pairs were tracked inside the lagoon, and one pair was followed for 63 h as the animals left Magdalena Bay and moved southward along the Baja California coast 213 km at a traverse rate of 3.4 km/h.

Mother-young pairs far back in the calving lagoon were found to move toward the deepest nearby water available on the outgoing tide, returning again after low water had passed. Aerial behavior consisted of breaching and spying out. In a breach the leaping animal rose two-thirds or more of its length from the water, falling back on its side. In our observations breaching seemed associated with the presence of males. Spying out was much more leisurely and often seemed to involve an animal with its flukes on the bottom, forcing its head out of the water. Contact between mothers and calves was very common; the calf often slid over the body of the mother and was lifted by the mother in conditions of stress. Floating whales seemed to be supported by inflated lungs which spread the loose rib cage apart producing a very flat cross-sectional profile. The spout was of seawater and it is speculated that part of its volume comes from water entering the nostrils as they open. Whales were observed grubbing in the bottom both in and out of calving lagoons, but feeding was not definitely confirmed. Mating was concentrated at lagoon mouths but some sexual behavior was noted inside lagoons. Female whales were found to be aggressive when their calves were disturbed, thrashing sideways with flukes at intruders, or attempting to hit a vessel with the flat of the flukes. Resonant clicks and loud broad band claps were recorded from calves as they were released to their mothers.

Pacific Mexican lagoons frequented by calving and breeding California gray whales, *Eschrichtius robustus* (Lilljeborg), are easily accessible by road and ship. Even so, information regarding the behavior of adults and young in these lagoons remains fragmentary. This paper describes behavior studies performed in January-February 1974 and 1975. Several methods were used. Observations of undisturbed whales were made from shipboard and skiff. Behavior was noted during capture sequences of nine young whales. Aircraft surveys were made. A set of sequential observations, principally of mother-young pairs, was made from a large dune (Colina Coyote) set on the edge of a major nursery channel. Finally, behavior of mother-young pairs was observed during radio tracking sequences on three animals. Data on diving depths and profiles, and water temperature, were also gathered during these tracks.

Captain Scammon's initial forays into Laguna Ojo de Liebre (Scammon's Lagoon) to capture whales resulted in the first record of the California gray whale from these lagoons, though the nature of his work certainly imposed disturbances that masked much behavior. Little was added for nearly a hundred years. Initial population counts were begun for the entire eastern Pacific population by Hubbs (1959), extended by Gilmore and Ewing (1954), Gilmore (1960a, b), Hubbs and Hubbs (1967), and Rice and Wolman (1971) and finally by Henderson (1972) and Gard (1974). Gilmore et al. (1967) added information about calving along the Sonora coast.

These studies revealed information regarding distribution of age-classes in the calving lagoons and features of behavior such as respiration, diving, swimming speeds, and aerial behavior.

Other studies have touched on several aspects of gray whale life. Huey (1928) and Wyrick (1954) gave field descriptions of behavior. Acoustic studies in Laguna Ojo de Liebre have been made by Eberhardt and Evans (1962), Poulter (1968), and Spencer (1973), while more general studies of mother-calf behavior have been made by Walker

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(1962) and Eberhardt and Norris (1964). Studies by White and Mathews (1956) and Spencer (1973) have given some information about physiological functions of the whales.

Henderson (1972) has reviewed historical data on the eastern Pacific gray whale fishery and speculated about previous distributions of numbers in the breeding population.

The capture of the suckling gray whale calf, Gigi, and her subsequent captivity and release revealed several new aspects of young gray whale behavioral and physiological biology. The various studies performed on Gigi were collated and edited by Evans (1974a).

Rice and Wolman (1971) have summarized data from all parts of the migratory path and their studies of 316 whales captured off San Francisco provide the best information on reproductive cycles and what might be called the migrant procession. They described the sequence occupied by various age and sex classes in the migratory column (see also Sund et al. 1974 and Leatherwood 1974).

The study reported here will draw from these works and add further information on feeding on southern grounds, mating, aggression, mother-calf relations, aerial behavior, respiration, and tidally related movement.

MATERIALS AND METHODS

During 1974, capture and tracking exercises were carried out using the 45-foot swordfish boat *Louson* under the direction of Captain Tim Houshar. In 1975, captures were performed from the *Orion* (Captain Peter Zimmerman) and tracking performed on the Scripps Institution RV *Dolphin,* a 95-foot motor vessel.

Tracks were performed using Ocean Applied Research (OAR) tracking radios, model PT-219, equipped with lithium batteries that generate a pulsed 50-ms/s signal each time the antenna rose above the surface.[4] Because the whip antenna had been broken on one radio when a young whale rubbed against the capture vessel during 1973 work, a flexible antenna equipped with a spring base was substituted in 1974. This minimized such antenna damage. Signals were processed with an OAR automatic radio direction finder and plotted on a strip chart recorder. In 1974, a multichannel sensing and digital recorder system developed by the Biotechnology Laboratory of the Franklin Institute, Philadelphia, Pa., was used to record water depth (pressure) and water temperature.

In 1975 a pressure recorder (TSK depth recorder, 0-1,000 m model) was used to record maximum dive depth.

Harnesses used in both years consisted of a stretchable nylon fabric harness, reinforced at appropriate points with heavy nylon straps. This material was fastened to a curved aluminum back plate which was protected beneath with neoprene sheeting to minimize abrasion to the animal (see fig. 3, Norris and Gentry 1974). Instruments and the tracking radio were mounted on the plate. A syntactic polyurethane foam float was molded to fit over these and painted bright yellow to aid visual sighting. This float provided about 0.5 kg of positive buoyancy to float the harness after jettisoning.

Release was achieved by two means. First, soluble machined magnesium bolts were used to give timed release of up to 6 days duration. One release during the 1975 expedition used a crystal timed explosive bolt system backed up by a soluble magnesium nut. The timing circuitry, which used a serially charged capacitor bank, released early because of a faulty magnetic switch.

The 25-m sand hill of Colina Coyote provides a fine site for observation of undisturbed whales. From it an observer can see a stretch of channel approximately 5 km long. Often animals within the area could be identified individually by scars and marks. Details of behavior such as spying out, respiration, and other features were observed (Figure 1).

This dune appears to be just north of the southern limit of most whale movement in the Boca Soledad area. A moderate number of animals passed the dune and swam a kilometer or so south toward the north end of Devil's Bend, a narrow winding channel flanked by tidal flats that ultimately connects to upper Magdalena Bay. During our observation period, we sighted no whales swimming into the narrow channel itself.

The channel in front of Colina Coyote is approximately 1,200 m wide, is bordered on both sides by tidal flats of variable width, and has a central channel of rather uniform depth, varying from about 8 to 10 m. Various landmarks were named by our observation team to permit easy notation and reference and are noted in the inset of Figure 1. A camp was established behind a small

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

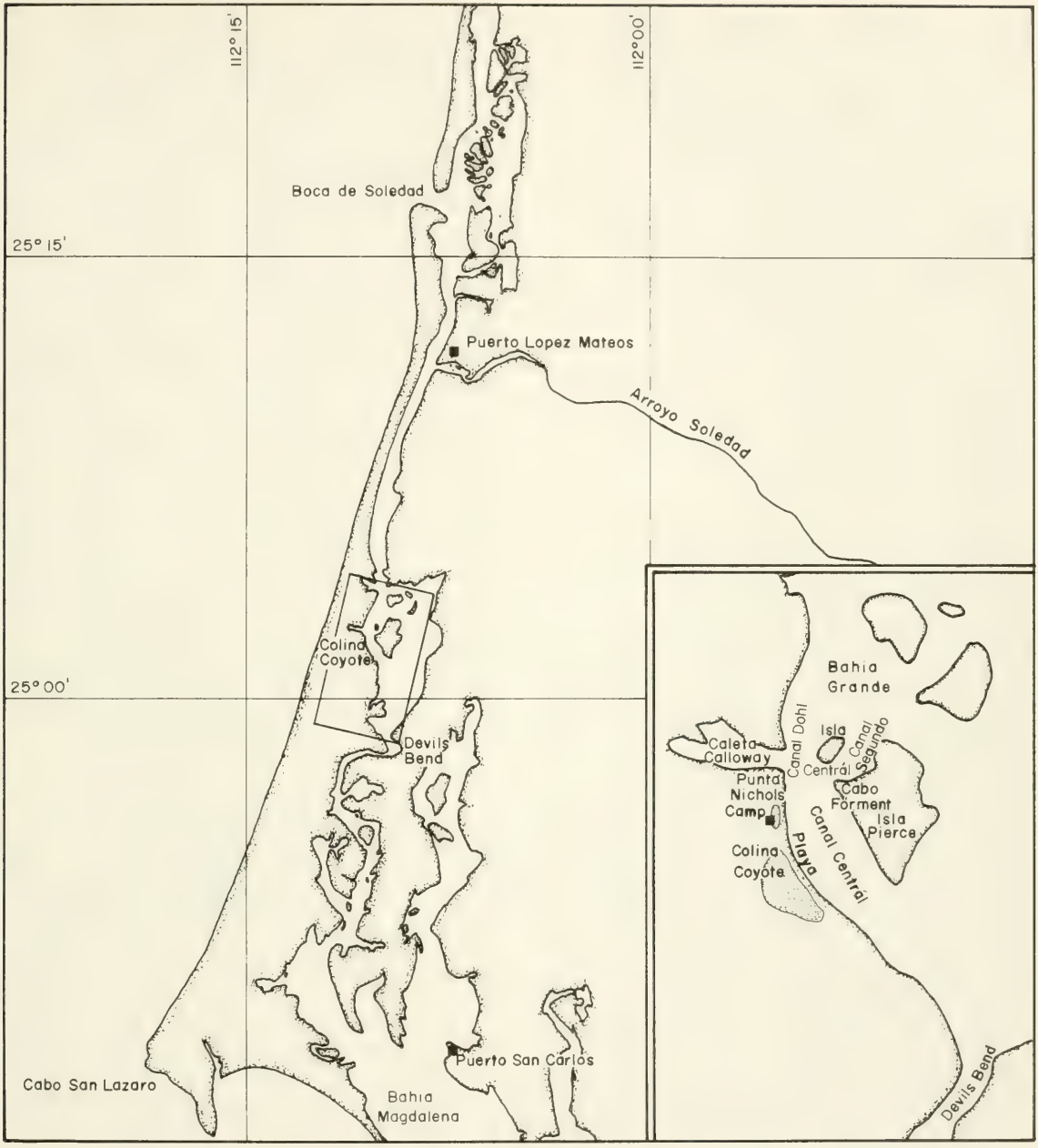

FIGURE 1.—Chart of the capture and study areas in Magdalena Bay area of Baja California Sur, Mexico. Calves were captured in the channel off Puerto Lopez Mateos, at Colina Coyote, and at Puerto San Carlos. Inset map shows area around Colina Coyote, where most observation was done, with names of topographic features given by the study team.

sand hill nearby to prevent undue disturbance of whales in the adjacent channel and to allow easy access to the top of the dune.

A standard assemblage of telephoto-equipped still and moving picture cameras, a spotting scope, binoculars, and watches was used in recording. Nighttime observations were assisted by use of a Zoomar image intensifying night vision scope.

Watches were kept with two observers each and daily observation of tidally related movements

and other features were made. Observations of aerial behavior, sound, respiration, and the relationship between mother-calf pairs were made. The sound recording system consisted of an Atlantic Research Corporation LC 32 hydrophone, with a response of ±4.0 dB over 0.1-100 kHz, a Hewlett-Packard 466A amplifier, and a Uher 4400 Report Stereo tape recorder with an upper flat frequency response of approximately 20 kHz at 7.5 ips. Signals recorded above 20 kHz are, at best, nonquantitative indications of energy at these levels and may also be instrumental in nature (i.e., the result of ringing in one or more parts of the system).

Counts of whales and their distribution were made both from shipboard and from aircraft.

RESULTS

Tracking Studies

Tracking experiments were designed for a maximum of 6 days and were intended primarily to test logistic systems and instrumentation for longer tracks. Nonetheless, examination of the data provides some insights into behavior in and out of the calving lagoons. Two animals were equipped with radio packs and the depth/temperature tape recorder units in the 1974 test series. (Details of the data system are in preparation and will be reported elsewhere.) The first whale calf (a 5.6-m total length male) was caught in Bahia Grande south of Lopez Mateos on 31 January 1974. During capture, its mother repeatedly rose beneath the captive which slid to either side off the rising body of the larger animal. The adult made no attempt to entangle the restraining line, nor was there any aggression noted toward the collecting vessel, which sometimes approached within approximately 15 m of the struggling pair. The animal, restrained by a single head noose that had cinched tight anterior to the pectoral fins, proved to be extremely strong and required 25 min of concerted effort by eight men to beach it. The harness was attached and the animal was quickly returned to the mother who patrolled in the nearby channel. This pair stayed in the lagoon for approximately 4 days. They first moved northward toward Lopez Mateos and then turned and swam southward through Bahia Grande, past Colina Coyote, and into the narrowing channel area north of Devil's Bend. They, however, did not enter this narrow (approximately 50 m wide) channel. Aboard the tracking vessel, we noted that the animals were effectively in a cul-de-sac, and that they would probably have to move northward to leave the lagoon via Boca Soledad. The vessel was therefore moved northward and moored near the fishing village of Lopez Mateos. During the night, the whale pair swam from Devil's Bend to Lopez Mateos (22 km) and passed the anchored vessel, stopping at a moderate-sized bay just inside Boca Soledad. The next day the animals returned downchannel past the vessel disappearing into the region of Bahia Grande where radio contact was lost. It was correctly assumed that they would not pass through Devil's Bend, but instead would remain in these southern channels. The collecting crew then caught a young female whale and instrumented it. This calf and its mother immediately moved northward out of the lagoon, through Boca Soledad, and began an ocean traverse southward just offshore of the barrier dunes. The crew was able to follow the pair by shipboard direction finder over the intervening dunes of Isla Magdalena for approximately 33 km south of Boca Soledad when contact was finally lost. That night the first cow and calf again came upchannel and passed the anchored vessel at Lopez Mateos moving toward the entrance at Boca Soledad. It is surmised that somewhere in this region the calf's harness cast loose, since a continuous signal was intermittently received. Only when the vessel moved into the Boca itself, clear of intervening sand hills, was the signal reacquired fully. Directional signals indicated that it was located approximately in the middle of the Boca, and probably washing back and forth with each tide change. It was later recovered on the beach 3 km north of the Boca, its instruments intact and operating.

For the 1975 tracking study a 5.3-m male calf was captured directly in front of Puerto San Carlos in upper Magdalena Bay, stranded on the beach south of the main pier, harnessed and released there. When released at 1105 h on 5 February, mother and calf reunited quickly and began moving rapidly toward the main part of Magdalena Bay. The pair skirted along the 20-m contour of the main bay until deeper water at the bay entrance (along Punta Redondo at the north tip of Santa Margarita Island) was reached at 0200 h, 6 February. The pair went directly into deep water past the point, out at least to the 100-m contour before curving back toward shore again at 0600 h. The depth recorder on the calf later showed that

the animals dove to or near the bottom during this traverse (maximum recorded depth 110±10 m). The impression given by the track at this point is that the animals were navigating to some extent by diving to the bottom and when the water deepened they turned for shallower inshore water. This is similar to the findings of Evans (1974b) for the instrumented whale Gigi released off San Diego which also dove to near the bottom and reached a maximum depth of 170 m.

Once near shore they skirted Punta Tosco at the southern tip of Santa Margarita Island, moving directly up the Rehusa Channel to a point off the middle of Isla Cresciente in quite shallow water at 1400 h. The animals remained there for 2 h and stayed almost constantly at the surface. Much rolling and throwing of pectoral flippers and flukes could be seen. We speculate that this interlude could have included a nursing sequence following the concerted swimming effort immediately after capture (Figure 2). After milling in the general area of Isla Cresciente at 0900 h, the pair began to move southward again, staying close inshore. At 0200 h the following night, the radio signal changed from the intermittent signal typical of a swimming and periodically surfacing animal to a constant signal, indicative of harness release. The harness was retrieved successfully at 0930 h. The track had covered 213 km in 63 h, for a traverse rate of 3.4 km/h, or 1.8 knots (2.1 knots excluding 20 ± h of quiescence) and had travelled 159 km southeast directly past the last calving lagoon on the Baja California coast.

One may speculate why the two instrumented animals that left the calving lagoon went south rather than in the expected northerly direction. The normal path at the beginning of northerly movement is not known. First, it seems possible that initial movement from the lagoon may incorporate some milling or nondirectional movement before migration begins. Second, the driving force which motivates and directs the northern migration may be involved. Is it hormonally stimulated, and timed by parturition and nursing? If so, what is the equivalent change in the male and how are these hypothetically related hormonal events related to path direction as well as to initiation of the migration itself? That is, does an animal have a general southward tendency of movement at one period that changes to north before normal migration back to Arctic latitudes? Third, could the attachment of instruments produce an initial direction aberration in path? In view of our observations of instrumented mother-young behavior within the lagoon itself, this appears unlikely, but further study of

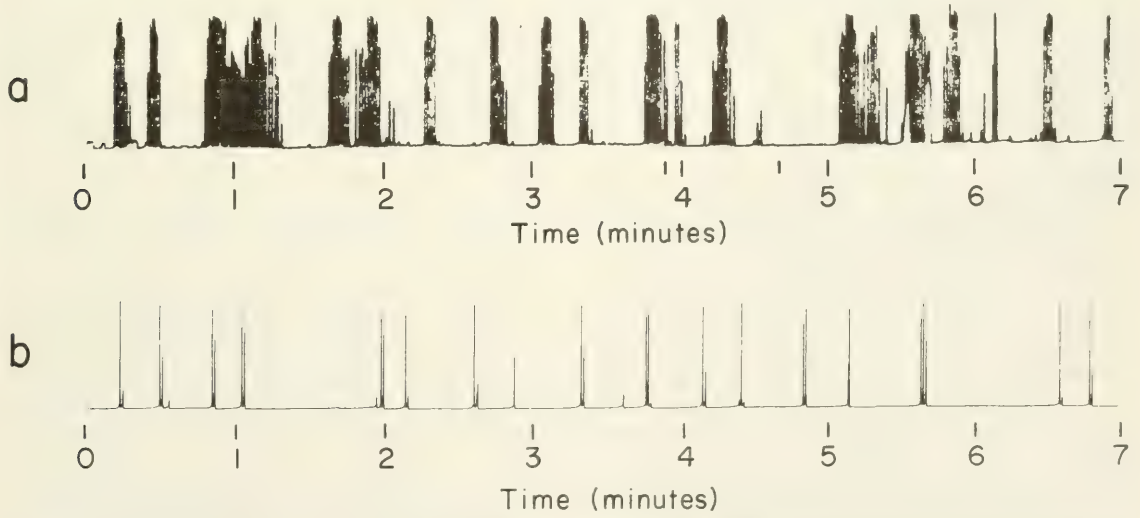

FIGURE 2.—Respiratory patterns of (a) a quiescent and (b) a swimming calf. The record in (a) was recorded off Isla Cresciente at the entrance to Almejas Bay, Baja California Sur, Mexico. This is the southernmost calving lagoon on the peninsula. The mother-calf pair lay at or near the surface in shallow water for 2 h. The repeated bouts of surface activity may represent nursing sequences. Each spike represents a radio transmission from the calf. These transmissions were given every second when the antenna broke the surface, and indicate an average of 16 s/min surface time. Amplitude of spikes varies with transmission efficiency. Time is in minutes. The record in (b) is for the same pair during normal swimming and indicates an average surface time of 3 s/min.

the initial southerly movement of both non-instrumented and instrumented animals appears in order.

Observation Studies

Behavior of Instrumented Animal — 1974

The depth record of the lagoon track of the male calf showed patterns quite different from those we have come to expect from cetaceans during radio tracking. The most striking difference was long periods (up to 3 h) when the calf apparently was at or very near the surface. Although instrumentation circuitry functioned properly in pre- and post-track tests, we prefer to wait for replicate tests to check the validity of these curious observations before reporting the results in greater detail.

Tidal and Water Depth Relations

Whales observed from Colina Coyote responded to the changing tide every day. Each time the high tide turned and while it was still high, many mother-calf pairs swam slowly northward into the extensive deeper water of Bahia Grande. Sometimes well before the tide was very low most animals would be gone from in front of Colina Coyote, with most stragglers travelling in the deepest water available (see Figure 3). The return movement began in similar fashion with the beginning of flood tide. The variation in arrival was so great that some animals did not appear until approximately high tide. Casual observations in channels in upper Magdalena Bay suggest that similar behavior may occur there, though in the deeper and broader waters of that open bay some whales were present throughout the tidal

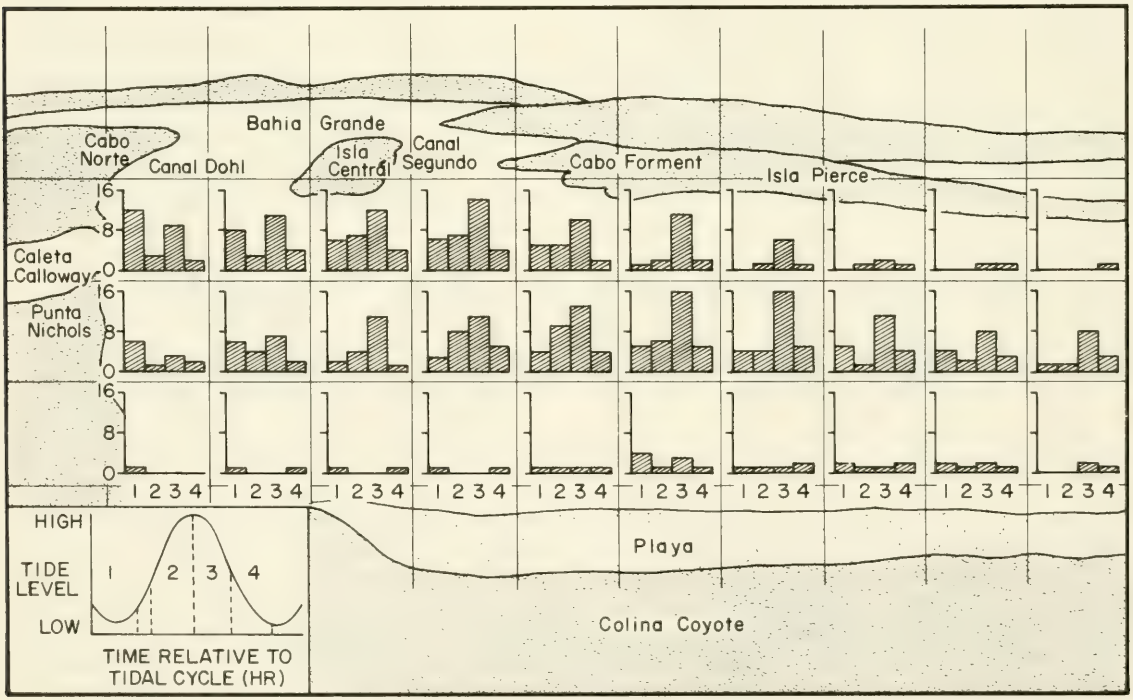

FIGURE 3.—Tidally related movements of adult gray whales in the calving lagoon at Colina Coyote, Baja California Sur, Mexico. Sketch map of waterways in front of Colina Coyote observation post showing tidally related movements of adult California gray whales. Data were acquired visually and recorded on a base map without the grid marks, as tracks against time. The grid was superimposed and an enumeration of sightings per square made for the time period involved. Animals entered or left on the turning tide, thus low tide (1) shows a concentration of animals in Canal Dohl, but also some deep in the Canal Central. The latter represent animals that entered the area soon after the change to incoming tide. Bars for high to 2 h after high tide (3) and 2 h after high to mid-low tide (4) reveal first a high concentration of animals coming up channel toward Bahia Grande and passing Colina Coyote, and finally a few stragglers making this passage before low tide. Animals seen in the period from medium rising to high tide (2) represent the more or less static population of animals that milled slowly in the channels in front of Colina Coyote before tidally related movement began.

cycle regardless of tide. Probably such behavior is an important means of avoiding stranding in the complicated shallower channels of calving lagoons.

Whales seldom leave the fairly deep channels, even at the highest tides. Much travel occurs along the channel edges but the animals seldom venture over tidal flats or sand bars, even those covered with 2 or 3 m of water. Occasionally, whales will venture over the edges of such flats when avoiding other whales or a pursuing vessel. The usual reaction to pursuit, however, is to seek deep water. An exception was produced by what we suppose were the pursuits of female whales by males. These chases, often involving three animals, sometimes went into water so shallow that the whales were nearly stranded. Very narrow channels are, however, avoided; we seldom saw whales traverse areas narrower than 130-140 m in width. Because the channel south of Colina Coyote in Devil's Bend is both narrow and sinuous and because we never saw whales there, we suspect it is not used and thus whales in Magdalena Bay are a separate group from those off Colina Coyote that use the Boca Soledad entrance to the sea.

Aerial Behavior

A controversy has long existed over the functions of the various kinds of aerial behavior exhibited by the gray whale (see, for example, Gilmore 1961, 1969; Walker 1962).

In our observations breaching is very different behavior from the much more leisurely spying out behavior (see also Walker 1962), and the two occur in quite different contexts. We use the term breaching to indicate a partial leap, often until two-thirds or more of the animal is free of the water, usually terminating with a rolling turn that causes the animal to reenter backward or on its side with a large splash that can often be seen for several miles. Breaches usually occur in sequences, often of three, and usually with decreasing vigor through the sequence. Gilmore (1961) reported seeing 11 breaches in a single sequence. A breach is vigorous, even violent behavior. We have watched many breaches and cannot report any being made by a cow with a calf, though Gilmore (1961) reported that mothers and calves sometimes breach. Instead, they seem to be made predominantly by rapidly moving animals that may be males or females in the company of males. It seems possible to us that such leaps represent sexually related displays, perhaps not unlike the breaches of such forms as humpback and male killer whales.

We have seen breaching most commonly at sea or in the seaward parts of lagoons where mating was common, although it was seen on three separate occasions in the deepest part of the Boca Soledad in front of Colina Coyote. On these occasions, it was performed by a swift-swimming unaccompanied animal that entered and caused some chases and agitation among the otherwise placid mother-calf pairs. Because of this creation of agitation among the nursing females, and because of its relatively small size, we suspect that it was a male.

In sharp contrast, a spy out is a leisurely event in which the animal raises its head slowly out of the water, often nearly to or slightly beyond the level of the eyes, and then slips back into the water as gravity causes it to fall slowly out of equilibrium. In shallow water, we believe spy outs are performed by an animal with its tail pressed against the bottom, and that flexing of the back forces the head out. Cows with calves often spy out, though single animals also exhibit the behavior. At Colina Coyote, spying out most often occurred in a rather tightly circumscribed sector at the edge of the channel from the middle of Isla Pierce north past Cabo Forment, Canal Segundo, and Isla Centrál, though it was seen occasionally in the middle of Canal Centrál (Figure 4). Soundings in this area showed a rather uniform depth of 8 to 10 m.

The eyes of the animals spying out were often below the waterline, and hence aerial vision was not always involved. Further, spying out was observed at night off Cabo Forment by use of a night vision scope. The observation occurred on a clear moonlit night. It is our strong impression that this kind of spy out is not related to viewing surrounding terrain or objects in air but is usually performed by nearly quiescent animals that may simply be making comfort or postural movements. We could not determine if it had any relation to nursing though we did see calves circling spying adults which suggests that nursing was not necessarily involved since the teats of the mothers were at least 6 m below the surface. The reverse behavior was occasionally seen, especially in Bahia Grande, in which an animal extended its tail into the air for a few seconds before subsiding back into the water, as if its snout was resting in the bottom mud.

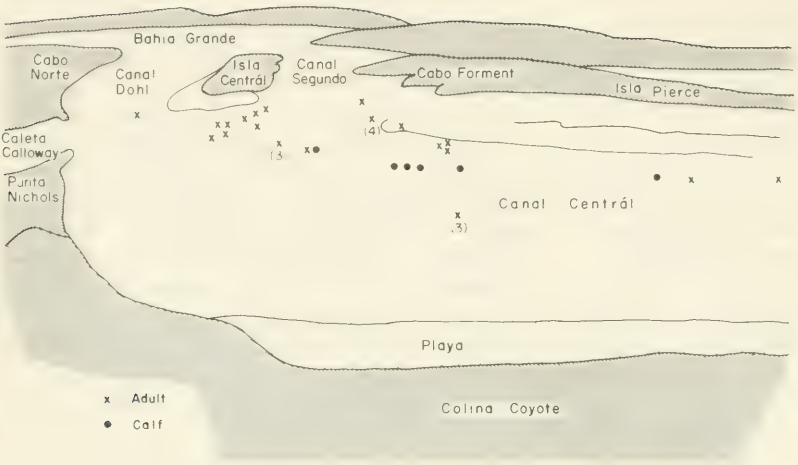

FIGURE 4.—Distribution of spy outs by adults and calves as noted from the Colina Coyote observation station.

Individual spy outs sometimes extend for rather long periods, another evidence that the animal is touching bottom at the time most of them occur. Nineteen examples ranged from 4 to 17 s duration with a mean of 7.6 s. In the longest, the animal rose from the water above the eyes, subsided until only the tip of its snout showed, and rose again to about the angle of the gape before slipping back again.

Occasionally spy outs occur in deeper water where a whale cannot be expected to touch and then the whale subsides very rapidly, just as would be expected of an unsupported animal in water.

Some spy outs do seem to involve aerial vision as has been suggested by Gilmore (1961). When an adult whale and calf are pursued, the adult may sometimes stop her flight and spy out. In one such case, the animal rose slowly and we could see its eyes. After such a spy out, the whale pair typically resumed avoidance behavior.

Of 52 spy outs recorded at Colina Coyote, 3 involved water coming from the corners of the whale's mouth. In two cases, off Cabo Forment, the released water was muddy. In one case, while the observer watched through a telescope, the whale rose with muddy water cascading out of the corner of its mouth. A similar instance was noted at Punta Tosco at the entrance to Almejas Bay in which an animal rose near the observer in a drifting skiff, its back toward the boat. As it rose, clear water gushed a foot out from the head from both lower mouth corners (Figure 5).

Thigmotaxis

One of the most striking behavioral attributes of mother-young pairs is nearly constant bodily contact in resting or passively floating animals. The contact seems to be solicited by both partners since the young often swims over the mother and is lifted as she raises head, body, or tail under the baby. Babies may slide over the mother from her head to her tail stock. In the course of such contact, the baby may roll onto its side or back, throwing its pectorals into the air. Lifting by the mother may force the baby calf out of the water even in a relatively quiescent pair.

In frightened animals, the lifting continues on a more violent scale as this excerpt from field notes (Norris) shows. "February 2, 1974. 1300: Bahia Grande. A calf was noosed and the line cinched tight around the pectorals. The calf was accompanied by a large barnacle-encrusted whale and shortly by another adult. They were the most violent consorts we had yet encountered, thrashing their tails and rolling over, repeatedly supporting the baby partly out of water. An attempt was then made to place a head net over the calf by inching the vessel's plank over the thrashing trio. Suddenly one flailed sideways sending a sheet of water over the bow. The head net was successfully placed and line slacked off, all three animals moving 50 m or so from the bow. Then one adult heaved its body into an incredibly powerful thrash of the tail, calf on top, causing the young animal to fly completely free of the water. Both head net and noose flew free."

On 1 February 1974 a young whale was captured and shortly after it was netted, the accompanying adult disappeared. Because we did not want the young animal to lose its parent altogether we released it as soon as it could be

FIGURE 5.—An adult gray whale spying out at the Rehusa Channel adjacent to Punta Tosco, Baja California Sur, Mexico. Note clear water gushing from both posterior mouth corners.

brought alongside, but it refused to leave the vessel. In fact, it pressed itself up against the hull, sometimes sliding under the stem or taking up station alongside the overboard discharge from the main engine. Every attempt to push it away with oars or brooms failed until the ship was finally backed in an arc away from the animal, leaving it following in our wake. Shortly, to our considerable relief, the adult was seen surfacing alongside the young animal. This thigmotactic behavior is strikingly reminiscent of that reported by Norris et al. (1974) for a humpback whale, *Megaptera novaeangliae*, baby in which a released young also refused to leave the side of the collection ship.

From time to time mothers with calves are engaged in rather violent chases with other adults which we speculate to be males. We observed one such chase near Lopez Mateos about 3 km inside Boca Soledad. These chases can be violent with much rolling and thrashing and long high speed sequences in open water, fast enough that the animals produce bow waves of some size. In one such chase we observed a baby racing along attempting to keep station with three adults. The next day in the same area a lone baby, perhaps the same animal, was noted partially stranded. This baby, apparently completely unharmed, swam ashore until its belly touched the sloping sand of the beach. We launched it repeatedly back into deep water without avail. It circled back into the shallows despite all our attempts and did so in both directions (and because it circled in both directions we did not feel it had a middle or inner ear orientation problem). Our impression was that the baby was seeking contact and thus stranding.

Buoyancy and Respiration

Passively floating or slowly moving adults in the calm lagoon areas allowed close inspection of some of the mechanics of respiration and of the formation of the blow or spout (see Kooyman et al. 1975). In such adults, breaths were sometimes taken with a few inches of the back exposed or with just the nostrils protruding. The area anterior to the nostrils swells before air is released, and adults often seemed to straighten or arch the back slightly causing a slight upward movement of the head prior to expiration. This did not always occur as sometimes an animal seemed simply to rise slightly prior to a blow and to subside after it.

Sometimes when a wholly quiescent whale blew, it raised its head slightly with the breath and slid backwards slightly just after it. In such quiet animals there seemed to be some internal mechanism by which the animal trimmed its buoyancy. It sometimes sank slightly after a breath or seemed to bounce slightly, rising a few inches to a new resting level.

Some breaths were released underwater both in the lagoons and out, and by both adults and young, usually causing a strong boil.

The gray whale spout is obviously double if viewed in front or behind the whale and may appear single from the side. It varies from a low "mushy spout" in breezy conditions to a fairly slender column perhaps as much as 2.5 m high in very calm air.

The spout is dense throughout its height from its initial exit point at the animal's nostrils to the top of the blow, and one can occasionally see the column of rushing air "tear" at the surrounding seawater entraining it into the blow as a ragged sheet. Most times the blow seemed to start just as the animal's nostrils rose to the surface and such adjacent seawater was obviously a considerable part of the blow. Occasionally, however, a floating animal did not sink down before a blow and a spout was sometimes not produced. It is our impression that in the calving lagoon most or all of the spout involved either water entrained in the column of rushing air from the sides as the animal's nostrils broke water or from a small amount of water pooled on nostrils, or perhaps more likely from the seawater that had entered the uppermost part of the nostrils just prior to the blow. Condensation is clearly an important part of the blow of whales breathing into cold air, as in more polar latitudes, but was not in our observations within calving lagoons. Neither whales that did not submerge between blows nor stranded calves spouted.

While spouts were taller and more evident in calm morning air, they were present throughout the day and at sea. Our impression is that visibility is affected by such changing conditions but that the mechanism of spout production in this latitude (25°N) remains the same. That is to say, wind may shorten the spout and make it harder to see but most respirations at sea produce spouts regardless of time of day.

Baby whales during swimming tend to toss their heads upwards when they blow, unlike adults, and as a result respiration breaks the smooth course of their swimming. This movement is extreme enough that one can sometimes see their lower jaws rise free of the water during respiration. Adults always seem to remain more deeply submerged with eyes and lower jaws well below the surface during spouting.

Patterns of respiration are quite different in mothers and young. One young animal observed moving slowly with an adult took 88 breaths/h while the attending adult took 58 breaths/h (Figure 6).

During what we suspect might be nursing sequences by an instrumented calf, surface times were considerably longer than otherwise, averaging 16 s/min as opposed to 3 s/min in travelling young.

During steady swimming the respiratory pattern becomes more regular, generally with a sequence of closely spaced blows followed by a longer period of apnea, with this sequence repeated over and over (Figure 2) (see also Wyrick 1954).

Often, adult whales were encountered floating absolutely passively in the calving lagoon. The back from about the nostrils to the base of the tail was often exposed. In such instances we were impressed by the very broad curve of the exposed back, as if the chest of the animal had a huge

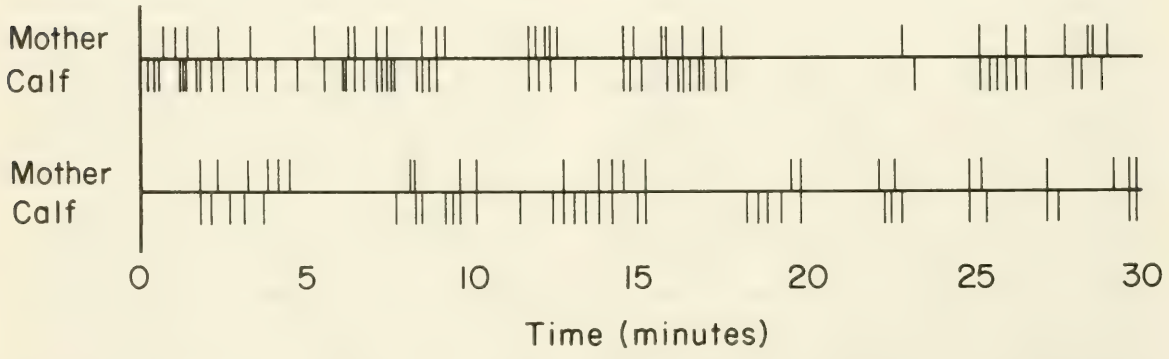

FIGURE 6.—Respiratory patterns of a California gray whale mother and calf pair swimming slowly off Colina Coyote, Baja California Sur, Mexico. Adult respirations equal 58/h; calf 88/h. Note that while initial respirations of a breathing sequence were sometimes simultaneous indicating surfacing together, often the calf surfaced first while the adult swam out of sight below the calf.

diameter. This broad abdomen narrowed immediately to the tail which seemed to be of normal diameter. In rapidly swimming animals the back often seemed much less broad. Our supposition is that in the passively floating animals the loose articulation of the rib cage allows the buoyant lungs to press the ribs outward, flattening the floating animal.

Feeding

Uncertainty exists with regard to the amount of feeding gray whales perform outside the Arctic feeding ground and especially in or near the calving lagoons. Both Gilmore (1969) and Rice and Wolman (1971) emphasized that nearly all migratory whales that have been examined had empty stomachs, while a few contained small quantities of gastropod opercula, wood, polychaetes, sand and gravel, ascidians, and hydroids. Matthews (1932) reported observations of gray whales feeding on shoals of *Pleuroncodes planiceps,* an anomuran swimming crab, or "red crab," off Magdalena Bay. Even so, Gilmore (1969:15) stated "one authoritative opinion holds that gray whales enter lagoons *primarily* to feed. The whales allegedly plow the lagoon bottoms in long furrows, exhausting first one section then another of the rich beds of eel grass and invertebrates. This opinion also asserts that the whale's high, vertical thrust of its head out of water—long considered a visual 'spy-hop'—is gravity swallowing, necessitated by his non-protrusible tongue."

Our observation of a whale spying out with mud cascading from the corners of his mouth at Colina Coyote is difficult to interpret (Figure 5). Surely the animal had grubbed in the bottom mud, but this does not assure that feeding had occurred. Nonetheless, at times we saw patches of muddy water around whales that were diving and spying out, indicating that much bottom grubbing was not isolated and perhaps common.

A more convincing observation was made by our flight observation team of Thomas Dohl and John Hall. They reported seeing 20 whales in shallow greenish water 75-300 m off the beach between Boca Animas and Boca Santa Domingo. Six of these animals were travelling slowly leaving muddy trails behind them. The trails were solid spreading wakes of muddy water and some of them were curved. They saw one whale surface and blow while continuing to trail such a wake, probably indicating that muddy water was issuing from its mouth. Their strong impression was of whales grubbing in the bottom producing the trails as they swam along. Once again we cannot be sure that these animals were feeding, but it is fair to say that probably with reasonable frequency whales in or near calving lagoons grub in the bottom mud or sand and take at least some of it into their mouths. Perhaps it is "pseudo feeding" as Gilmore (1969) suggested, but it is also possible that limited feeding does occur in or near the calving lagoons.

Population Segregation

We can confirm the long standing observation (Gilmore 1961) that at lagoons population segregation of a marked sort takes place. Mother whales with newborn young are indeed confined largely to inland waters within the lagoon systems. Single animals are rather uncommon there. Aggregations of whales without calves are common at or near entrances and in the nearby offshore waters. A considerable percentage of these animals is found in groups of two to six animals and much rolling, fluking, throwing of the pectorals, and bodily contact can be seen. Occasionally a protruded penis was noted as a whale rolled on its back and more often the perineal sheath of the male could be seen in such circumstances. Groups at bay mouths typically contained many moderate size animals, which we estimated at 10-12 m long. It seems probable that both yearling, juvenile, or young adults of both sexes and older males were involved.

All whales found south of the southernmost calving lagoon at Almejas Bay seem to represent this mixed group of males, yearlings, or nonparturient animals. The large group of animals seen around Cabo Falso and Cape San Lucas was of this type with no small young of the year being noted.

Aggressive Behavior

Gray whale aggression has been the subject of some controversy. Hand whalers reported aggression toward whale boats from animals harpooned in the lagoons (Scammon 1874). Later, some research workers have had boats damaged in encounters with whales. Nonetheless, suspicions existed that these encounters were due to the thrashings of a very large innocuous beast in

shallow water. Gilmore (1969), for one, reported no aggression from unprovoked whales during his work in the calving lagoons. We can lay these suspicions to rest. Female gray whales separated from their young are apt, indeed, to be vigorously aggressive. But like Gilmore, we have never seen aggression from unprovoked whales. Two examples from our field notes will suffice.

During capture the female stays in close attendance with the young, often placing herself between the baby and the shore line party. She sometimes pressed against the young, literally yanking the line from line handlers. These thrashings increased in intensity as the baby neared the shelf and it is our opinion that the mother was very dangerous at this time. We have always taken care to work with the baby 20 m or so into shallow water where the mother could not come. She patrolled the shelf edge at this time in water just deep enough to allow her passage and she even partially stranded herself. When the baby was taken into very shallow water or far over a flat, the mother sometimes wandered away. We presume this to indicate a loss of effective acoustic communication.

During one capture a line handler allowed himself to come within a few meters of the shelf beyond which the mother patrolled. She reared up, swung her flukes laterally just at the water's edge, with sufficient force that a sheet of water was sent over the entire work party. The blow missed the nearby line handler by a couple of meters but none of us doubted that it would have done serious injury if it had hit him.

On another capture, a young animal was stranded and the scientific party had worked on harnessing the animal for perhaps 20 min when the mother wandered away. The collection vessel had been given the task of keeping the mother close to the shore party by maneuvering around her. The ship was standing by 1 km to the south and about 0.5 km off the channel edge during stranding and then moved up to within about 100 m of the shore party to herd the mother whale while we harnessed the calf. The adult disappeared below the surface for about 45 s and came up under the stern of the vessel, hitting the hull so hard that the vessel was lifted up about a meter and heeled over 25°-30° to starboard. The whale's tail swung up in the air astern, with the broadside of the flukes toward the ship and approximately 2 m of the tail extended above water. The captain put the ship full speed ahead at about 12 knots and attempted to elude the whale. The whale followed below the vessel and three times rose to hit it, swinging her flukes up above water astern even though in full chase. The vessel ran in broad circles and finally swung over fairly shallow water, and at the same time threw seal bombs into the water (firecrackers used to disperse sea lions from fishing nets). The whale moved away at this point, after a chase of 5 to 7 min. The ship was largely undamaged except for a slightly bent propeller blade. The captain felt that the fast maneuvering prevented serious damage to the vessel.

Phonation

Evidence has been accumulating in recent years that the gray whale produces a number of different sound signals, including grunts, pulses, clicks, moans, bubble-release sounds, knocks, and rasping pulses. These sound records have been reviewed by Poulter (1968) and by Fish et al. (1974), and the latter workers recorded the sound of the yearling captive gray whale Gigi. These authors suggest that the metallic pulses recorded from Gigi may have been associated with the internal flow of air bubbles, since no air was released during the sound emission. They also reported click trains released by feeding gray whales, which consisted of clicks with principal energy from 2 to 6 kHz and duration of 1.0-2.0 ms, with a click repetition rate of 9.5 to 36.0/s. Similar click trains have been recorded by us in the channel near Lopez Mateos. In addition, we can directly attribute two kinds of sounds in whale calves since both were heard or recorded directly from these animals as they lay partially out of water; these were repeated low pulses and a very loud bang or intense click.

Low resonant pulses, which were not recorded, were emitted by a stranded calf on 27 January 1973 during harnessing. Each was a second or less in duration, emitted each 2-3 s, and concurrent with such emission one could see slight movement of the animal's body surface behind the head on the lateral body surfaces. No air was released during emission. This young animal was emitting pulses when reintroduced to the bay. The mother had wandered off some 300 m down channel by this time and as the baby swam across channel, the mother was seen to throw her flukes twice and then swim directly toward the distant baby. As they met, the mother slashed the water rather violently with her flukes, circled the baby and the

pair swam off together. Because of the distance involved at reentry of the calf and the rapid reunion, we assume acoustic communication was involved, perhaps the pulses mentioned above.

The sharp clicks were made by two male calves, on 2 and 5 February 1975, as they lay stranded at Puerto San Carlos, upper Magdalena Bay. Prior to click production the blowholes were pursed, giving the impression the animal was about to blow, but it did not, and no air was released. Instead it tossed its head slightly upward causing the slightly opened jaws to clap closed quickly (movement of the throat also seemed involved), at which point the click was produced. These signals were very intense and could be heard for long distances underwater; Bartley Gordon, who recorded the sounds for us, could hear them very clearly at least 500 m from the stranded animal. In each case, as the calf was released, clicks were heard before the mother and calf rejoined. Low pulses or grunts were also recorded from one animal.

In the 5 February release, the mother whale swam approximately 500 m southwest of the point at which the young was released. The baby swam resolutely down channel and the mother was noted taking up a collision course. Until the moment of contact sharp clicks were recorded, and then, as the whales met in a flurry of lunges partway out of water, the clicks ceased altogether.

These clicks vary from those recorded by Fish et al. (1974) in that we noted no long trains of closely spaced clicks, but instead sporadic signals given at a maximum rate of 2/s, but more often alone. The signals we recorded seemed to be of much higher intensity and of much broader band character than those noted by Fish and his colleagues. Further, their duration was about 0.25 s as opposed to 1-2 ms. In the sound spectrogram shown in Figure 7, a very intense broad band signal is portrayed, perhaps of frequency range extending well above the flat response band of our instrumental system (0.1-20 kHz). One wonders if these clicks bear any relation to the "earthquaking" reported by Ray and Schevill (1974).

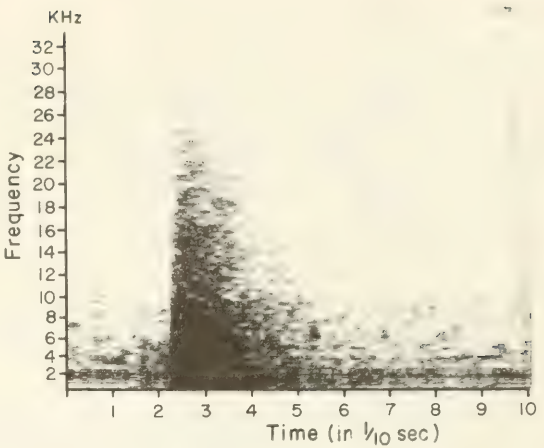

FIGURE 7.—Intense broad band "clack" emitted by a stranded gray whale calf at Puerto San Carlos, Baja California Sur, Mexico, on 5 February 1975. Effective analyzing filter band width is 45 Hz. Due to the limits of the recording system (about 1-20 kHz flat response) the signal recorded above 20 kHz indicates only some energy in that region, not its amount.

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We were helped with many logistical and official details ashore by Señor S. Serrano of the cannery at Lopez Mateos, Felix Armas Ortiz, Port Captain of Puerto San Carlos, and Carlos Martinez Toscano, of *Conasupo,* San Carlos, deserve special mention. Our work would have been very difficult without their assistance.

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DISTRIBUTION AND DURATION OF PELAGIC LIFE OF LARVAE OF DOVER SOLE, *MICROSTOMUS PACIFICUS;* REX SOLE, *GLYPTOCEPHALUS ZACHIRUS;* AND PETRALE SOLE, *EOPSETTA JORDANI,* IN WATERS OFF OREGON

WILLIAM G. PEARCY,[1] MICHAEL J. HOSIE,[2] AND SALLY L. RICHARDSON[1]

ABSTRACT

Dover and rex sole larvae attain an exceptionally large size and have a long pelagic life. Dover sole larvae (9-65 mm standard length) were collected in mid-water trawls and plankton nets during all months of the year. Judging from growth of larvae and occurrence in bottom trawls of recently metamorphosed juveniles, Dover sole are pelagic during their first year of life. Large larvae (50-65 mm standard length) are probably pelagic for over a year and few apparently are recruited to benthic populations. Dover sole larvae were most common in oceanic waters beyond the continental slope and in the upper 50 m of the water column.

The rex sole larvae captured were 5-89 mm long. Average size and stage of development of larvae increased from March through February, and juveniles were common on the bottom during winter on the outer shelf. Thus the pelagic phase usually lasts about a year. Both rex and Dover sole may utilize the outer continental shelf-upper slope region for a nursery during early benthic life.

Petrale sole larvae (10-22 mm standard length) were rare. They were collected only from March to June and appear to have a pelagic life of about 6 mo. Age-group 0 juveniles, uncommon in bottom trawl collections, were only captured on the inner continental shelf in the fall.

Dover sole, *Microstomus pacificus;* petrale sole, *Eopsetta jordani;* and rex sole, *Glyptocephalus zachirus,* are commercially important flatfishes of the northeastern Pacific. They ranked first, third, and fourth respectively in 1973 Oregon flatfish landings (Bruneau et al.[3]). Despite the abundance of Dover, rex, and petrale sole in bottom trawl catches, their larvae are not common in plankton or mid-water trawl collections (Table 1; Ahlstrom and Moser 1975).

Dover sole apparently spawn in specific sites in offshore waters deeper than 400 m (Hagerman 1952; Demory[4]). Rex sole, which do not appear to have specific spawning sites, spawn between the 100- and 300-m depth contours (Hosie[5]). Petrale sole are known to spawn in fairly well-defined locations in deep water (Ketchen and Forrester 1966; Alderdice and Forrester 1971). The rarity of Dover and rex sole larvae may be partially due to their reproductive strategy of producing relatively low numbers of large eggs (Table 2). Although development time to hatching is unknown, it is probably long for both Dover sole and rex sole. Petrale sole, on the other hand, produces smaller eggs in greater numbers; yet petrale larvae are perplexingly rare (Table 1). The incidence of larval capture of these three species certainly does not reflect their abundance as adults.

Larvae of two of these pleuronectids are unusual because they attain a large size. The genera *Microstomus* and *Glyptocephalus* both have giant larvae. Metamorphosis of *Microstomus kitt* and *M. pacificus* larvae takes place at lengths over 30 mm (Norman 1934; Hagerman 1952), and *M. pacificus* larvae 50 to 60 mm long have been collected (Table 1; Ahlstrom and Moser 1975). We are not aware of published reports on the size at metamorphosis of *Glyptocephalus zachirus* larvae although Ahlstrom and Moser (1975) stated that it is not unusual to collect larvae that are 50 to 60 mm SL. Metamorphosis in the congeneric *G. cynoglossus* and *G. stelleri* occurs at 40 to 60 mm in length (Pertseva-Ostroumova 1961; Okiyama 1963).

Because they attain a large size, Dover and rex sole larvae presumably have long pelagic lives. Hence they may be susceptible to dispersal and drift by currents for many months, a factor that

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[3]Bruneau, C., J. M. Meehan, and J. Robinson. 1974. Groundfish and shrimp investigations. Annu. Rep. 1973, Fish. Comm. Oreg., 25 p.

[4]Demory, R. L. 1975. The Dover sole. Oreg. Dep. Fish. Wildl. Inf. Rep. 75-4, 4 p.

[5]Hosie, M. J. 1976. The rex sole. Oreg. Dep. Fish. Wildl. Inf. Rep. 76-2, 5 p.

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TABLE 1.—Summary of captures of larvae of *Microstomus pacificus*, *Glyptocephalus zachirus*, and *Eopsetta jordani* from mid-water trawls and plankton tows in the northeast Pacific.

Study	Location	Time	No. hauls	No. hauls with Pleuronectids	No. hauls with *Microstomus*	No. hauls with *Glyptocephalus*	No. hauls with *Eopsetta*	No. larvae taken	No. Pleuronectid larvae	No. *Microstomus* larvae	No. *Glyptocephalus* larvae	No. *Eopsetta* larvae
Aron[1]	Calif. to Alaska	July-Sept. 1957 June-Oct. 1958	564	67	24	10	0	7,400	232	66 (14-64 mm)	12 (15-77mm)	0
Porter (1964)	Northern Calif.	Jan. 1959-Jan. 1964	59	21	0	4	2	[2]192	154	0	10 (25-62 mm TL)	2 (21-22 mm TL)
LeBrasseur[3]	NE Pacific	1956-59	~3,000	70	30	9	0	1,287	98	35	13	0
Waldron (1972)	Oreg. to B.C.	Apr.-May 1967	88	19	4	4	0	4,577	626	4	10	0
Naplin et al.[4]	Wash. to B.C.	Oct.-Nov. 1971	30	3	1	1	0	343	14	1	1	0
Richardson (1973)	Oreg.	May-Oct. 1969	354	52	9	18	4	55,049	123	10 (12-61 mm SL)	31 (22-89 mm SL)	4 (13-21 mm SL)
This study												
Bongo transect	Oreg.	Jan. 1971-Aug. 1972	287		32	41	1	23,578		75 (5-26 mm SL)	107 (4-67 mm SL)	1 (20 mm SL)
Bongo grid	Oreg.	Mar.-Apr. 1972, 1973 Mar. 1974, 1975	306		36	75	1	34,029		51 (4-21 mm SL)	181 (5-24 mm SL)	1 (18 mm SL)
Mid-water trawls	Oreg.	1961-74	~2,200		313	199	25			568 (9-65 mm SL)	360 (11-89 mm SL)	44 (10-22 mm SL)

[1]Aron, W. 1960. The distribution of animals in the eastern North Pacific and its relationship to physical and chemical conditions. Dep. Oceanogr. Univ. Wash. Tech. Rep. 63, 65 p.
[2]Flatfishes only.
[3]LeBrasseur, R. 1970. Larval fish species collected in zooplankton samples from the northeastern Pacific Ocean 1956-1959. Fish. Res. Board Can. Tech. Rep. 175, 47 p.
[4]Naplin, N. A., J. R. Dunn, and K. Niggol. 1973. Fish eggs, larvae, and juveniles collected from the northeast Pacific Ocean, October-November 1971. NOAA-NMFS, Northwest Fish. Cent. MARMAP Surv. I Rep. 10, 39 p. + 121 tables.

TABLE 2.—Egg diameter and fecundity of Dover, rex, and petrale sole.[1]

Species	Egg diameter	No. eggs/female
Dover sole	2.04-2.57 mm	51,900 at 42.5 cm 265,800 at 57.5 cm
Rex sole	1.98-2.34 mm	34,191 at 36 cm 238,144 at 59 cm
Petrale sole	1.21-1.25 mm	400,000 at 42 cm 1,200,000 at 57 cm

[1]Data from Hagerman 1952; Harry 1959; Alderdice and Forrester 1971; Hart 1973; Hosie 1975; Ahlstrom and Moser 1975; J. R. Dunn and N. A. Naplin pers. commun.

may affect survival and subsequent year-class strengths of these species which are known to be variable (Demory and Hosie[6]).

COLLECTIONS

We examined the catches of 593 bongo net tows and over 2,200 Isaacs-Kidd Midwater Trawls taken off Oregon to provide information on the distribution, dispersal, and length of larval life of these three species. The bongo nets had 70-cm mouth diameters with 0.571-mm mesh nets. Tows were made obliquely through the water column from the bottom or 150 m to the surface at a speed of 2-3 knots. Two data sets were examined. One set consisted of 287 samples collected on an east-west transect off Newport, Oreg., at stations 2, 6, 9, 18, 28, 37, 46, 56, 65, 74, 93, and 111 km from the coast (Figure 1). Samples were taken every month from January 1971 to August 1972 except January and February 1972. The other set consisted of 306 samples collected along 12 transects between the Columbia River and Cape Blanco, Oreg., with stations located 2, 9, 18, 28, 37, 46, and 56 km from the coast. Samples were taken in March and April 1972 and 1973, and March 1974 and 1975. Not all stations were sampled on each cruise.

Isaacs-Kidd Midwater Trawl collections were made with trawls having a mouth width of 1.8, 2.4, and 3.1 m, a 5-mm (bar measure) mesh, and a 0.5-m diameter cod end of 0.571-mm mesh at stations 28, 46, 84, and 120 km offshore (Figure 1). Stations from 158 to 306 km offshore (at 37-km intervals) were sampled less frequently. Tows were mainly taken along four transect lines perpendicular to the coast (Figure 1) during

[6]Demory, R. L., and M. J. Hosie. 1975. Resource surveys on the continental shelf of Oregon. Fish Comm. Oreg., Annu. Rep. July 1, 1974 to June 30, 1975, 9 p.

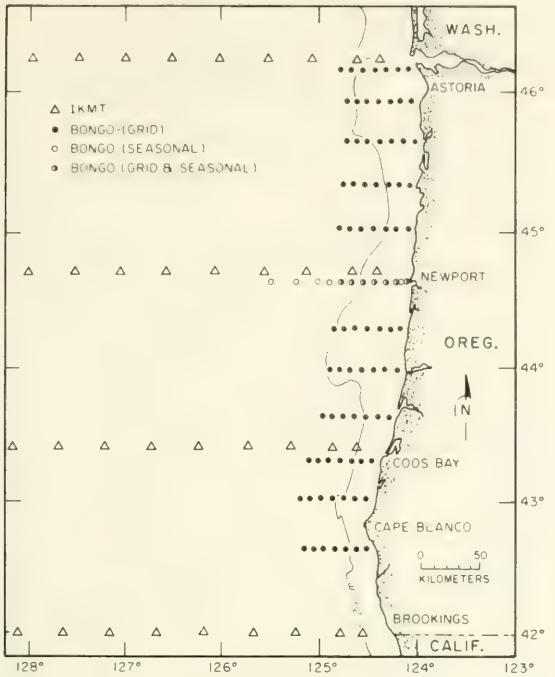

FIGURE 1.—Location of sampling stations off Oregon.

1961-69. These tows were generally oblique from 200 m (depth permitting) to the surface at a speed of 5-6 knots. A series of opening-closing mid-water trawl collections (Pearcy et al. in press) was also made 100-150 km off Newport within the upper 1,000 m during 1971-74. Considering all the collections, all seasons were sampled about equally.

Benthic fishes were sampled with a 3-m beam trawl (with 13-mm stretch mesh) on nine cruises during all seasons over the continental shelf off central Oregon (115 collections) and with a 5-m otter trawl on monthly cruises from January 1971 to August 1973, 7 to 11 km off Newport.

LARVAL STAGES

Standard length (SL) of larvae was measured to the nearest millimeter. Larvae were assigned to an arbitrary developmental stage depending primarily on position of the left eye:

Stage I: Larvae symmetrical. Left eye has not yet begun to migrate.

Stage II: From time left eye has begun to migrate to time it is on middorsal ridge of head. The eye is considered to be on the middorsal ridge when a line extended forward from the dorsal fin transects any part of the eyeball for Dover and petrale sole, or when such a line transects the middle of the eyeball and the eyeball itself is directed upward for rex sole.

Stage III: Left eye is on middorsal ridge as defined under Stage II. For Dover sole, this stage was divided into two parts on the basis of pigment pattern, which appeared to correlate reasonably well with eye migration.

Stage IIIa: Five or six dorsal and four or five ventral horizontally elongated streaks of pigment along the central body musculature.

Stage IIIb: Dorsal and ventral pigmentation streaks along the central body musculature joined to form continuous lines.

Stage IV: Left eye fully on the right side of head, so that a line extended forward from the dorsal fin does not transect any part of the eyeball.

In Dover sole, the left eye begins to migrate as notochord flexion begins, and the caudal fin is completely formed by the time the eye reaches the middorsal ridge.[7] In rex sole, however, the caudal fin forms completely while the eyes remain symmetrical. Limited evidence suggests petrale may be like Dover sole in this respect.

GROWTH AND DEVELOPMENT

The number and length of larvae assigned to developmental stages (Table 3) shows that each stage often included a wide range of sizes. Most of the Dover sole captured were stage I in bongo nets, and metamorphosing stage IIIa larvae in mid-water trawls. Only a few larvae 30-40 mm SL were captured, resulting in a bimodal size-frequency distribution. This may be a sampling artifact due to the unavailability of intermediate-sized larvae to our sampling methods, or it may be caused by rapid growth between stages IIIa and IIIb. A

[7] We found one abnormal Dover sole larva, a 43-mm SL tailless fish collected 125 miles off Newport, Oreg., in February 1964. This lack of caudal fin condition has also been reported for post-metamorphosed Dover sole (Demory 1972a).

TABLE 3.—The number and lengths of *Microstomus pacificus, Glyptocephalus zachirus,* and *Eopsetta jordani* larvae in assigned developmental stages, I to IV. Numbers in parentheses denote catches in bongo nets, excluding grid tows; numbers without parentheses are mid-water trawl catches.

Standard length	*M. pacificus*					*G. zachirus*				*E. jordani*			
(mm)	I	II	IIIa	IIIb	IV	I	II	III	IV	I	II	III	IV
4-5	(7)					(5)							
6-7	(38)					(28)							
8-9	(10)	2				(41)							
10-11	(4)	13 (2)	6			1 (5)				1	1		
12-13		10 (6)	20			1 (2)				1	3		
14-15		8 (4)	55 (1)			(2)				1	1		
16-17		2 (1)	90			(4)					1	12	
18-19		1	72			3 (1)						12	
20-21			79 (1)			4 (1)						8 (1)	1
22-23			45			3						2	
24-25			25			5 (2)							
26-27			16 (1)			3 (2)							
28-29			11			3							
30-31			7			8 (2)							
32-33			1			8 (1)							
34-35				2		7 (1)	1						
36-37			3			9							
38-39			1	3		13 (1)							
40-41				3		14 (1)	4						
42-43				2	2	8 (1)	6						
44-45				4		7 (3)	3 (1)						
46-47				4	4	6	4						
48-49				2	6	4 (1)	5	1	1				
50-51				5	11	6	10		3				
52-53				6	12	7	9		5				
54-55				5	5	3	3 (1)	2	5				
56-57				5	5	1	5	1	3				
58-59					3	3	10	1	3				
60-61				6	4	2	7	2					
62-63				1			8	1					
64-65					1		9	1					
66-67							1 (1)						
68-69						2	1	1					
70-71							4						
72-73							2	1					
74-75								1					
89							1						
Totals	(59)	36(13)	431(13)	48	53	131(104)	93(3)	12	20	3	6	34(1)	1

progression of increasing size with later developmental stages is apparent from stages I through IIIa, but little growth in length is evident between stage IIIb and IV. Larvae over 40-50 mm SL included both partially metamorphosed individuals with the left eye on the dorsal ridge and little pigmentation on the right side, and fully transformed individuals with heavy pigmentation on the eyed side. The largest larva was a partially metamorphosed individual of 65 mm.

Most rex sole larvae were classified as premetamorphosed stage I. This stage included a surprising length range, from 4 to 69 mm. Most of the growth in length apparently occurs during stage I before the left eye begins to migrate. The median length of stage IV larvae was actually shorter than that of stage II or III, suggesting reduction in length during metamorphosis. The largest larva was 89 mm (see Richardson 1973), apparently a record for any species of *Glyptocephalus*.

Petrale larvae occupied a small length range compared with Dover and rex sole larvae. Most of the larvae were stage III. Larvae smaller than 10 mm were never taken.

SEASONALITY, GROWTH, AND LENGTH OF LARVAL LIFE

The relative abundance of the stages of Dover sole larvae collected during different months in bongo nets and mid-water trawls is illustrated in Figure 2. Stage I larvae were the predominant stage in the bongo net catches from March to July; stage II larvae were most common during the summer (bongos) and fall (mid-water trawls), suggesting a progression of larval stages from spring to fall. The continuation of this trend is not apparent from the catches of stage IIIa larvae, the most abundant developmental stage during all months in mid-water trawl catches. Stage IV were most common during fall and winter months.

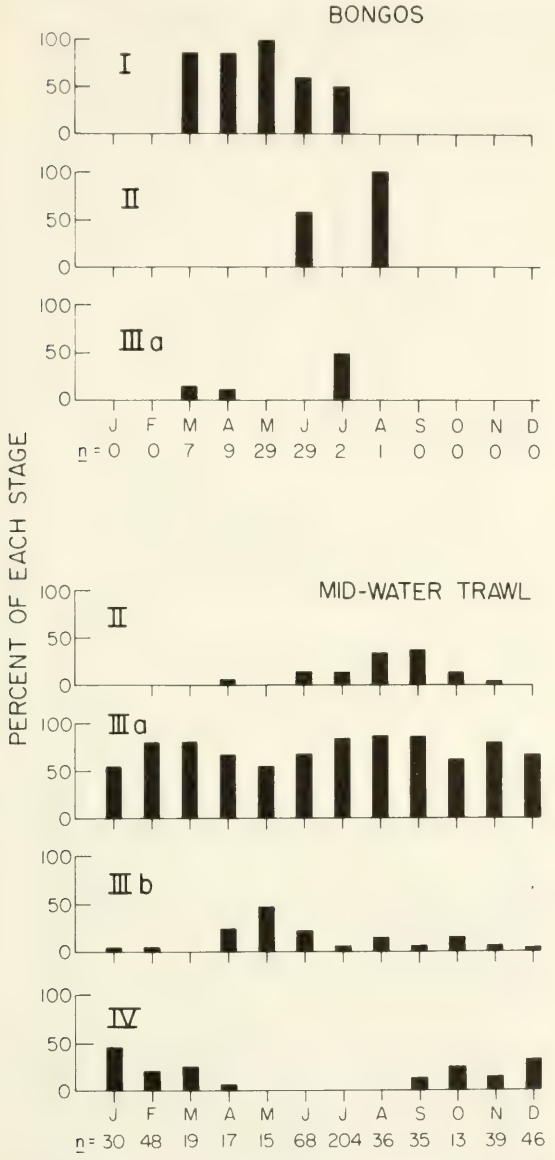

FIGURE 2.—The relative abundance of each stage of Dover sole larvae in bongo transect and mid-water trawl collections during all months.

Dover sole are known to spawn off Oregon primarily in winter, November through March (Hagerman 1952; Harry 1959), when stage III and IV larvae were present. It appears that Dover sole larvae are pelagic for at least a year. The large proportion of stage IIIa larvae during all months is puzzling, since relatively few of this stage would be expected during the winter and early spring if the larval period lasts a year or less.

Interpretation of growth and length of larval life is facilitated by the length-frequency data in Table 4. A trend for increasing average size of larvae is evident from April of one year to March of the next year for larvae <30 mm SL. This suggests growth only to at least 20-30 mm during the first year of life, and a pelagic life that lasts at least a year. No growth trends are apparent for large larvae, which were present all months of the year. Our interpretation of these data is that larvae begin to settle out at 30-50 mm and metamorphose after about 1 yr. Juvenile Dover sole of 40 mm have been captured in bottom trawls in February off Oregon. Possibly few 30- to 40-mm larvae were available to our gear because they were close to the sea floor. Larger larvae (>50 mm) may then represent a residual pelagic population that has not had an opportunity to begin benthic life, perhaps because they resided in water too deep during the period of settlement of most larvae. Information on the size and seasonal occurrence of juvenile Dover sole on the bottom, discussed in a later section, supports these contentions. Such an extended period of pelagic life after 1 yr suggests that Dover sole larvae may delay metamorphosis and settlement to the bottom if favorable conditions are not present, a phenomenon known for some benthic invertebrate larvae (Wilson 1968) but to our knowledge not for any fishes.

Mearns and Gammon[8] also reported Dover sole larvae year-around in waters off southern California with peak numbers in July. They showed a distinct growth trend from about 5-9 mm SL in April to 35-50 mm in October, suggesting that larvae may attain a size of 50 mm or larger during the first year of life. Ahlstrom and Moser (1975) collected Dover sole larvae chiefly during April through July off California.

The trends for rex sole are more readily interpretable than those for Dover sole. Rex sole were also captured in every month, but a progression of stages was obvious through the year (Figure 3). All larvae collected in March, April, and May were stage I, and all were stage IV by the following February. Since rex sole spawn off Oregon from January to June (Hosie 1975), pelagic life apparently lasts about a year. The presence of stage IV larvae in November and December and

[8]Mearns, A. J., and R. Gammon. A preliminary note on multiple recruitment of Dover sole populations (*Microstomus pacificus*) off Southern California. Unpubl. manuscr., 7 p. Southern California Coastal Water Research Project, 1500 East Imperial Highway, El Segundo, CA 90245.

TABLE 4.—Length-frequency distributions of *Microstomus pacificus* larvae collected during various months. Numbers in parentheses denote larvae caught in bongo nets; numbers without parentheses denote larvae caught in mid-water trawls.

Standard length (mm)	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
4-5	(1)		(2)									(3)
6-7	(7)	(23)	(5)									(3)
8-9		(3)	(7)	2								
10-11	1	(1)	10(4)	6(1)	1							
12-13		1	9(6)	19	1							
14-15	1	2	15(4)	33(1)	6	4	1	1				
16-17		1	13	59	4(1)	3		4	5	1	2	
18-19	1	1	3	35	4	6	2	10	5	2	4	
20-21	1(1)	2	3	21	5	9	3	10	8	4	9	3
22-23				10	6	4	2	4	3	4	9	3
24-25	1		1	5	1	1		1	6	1	6	2
26-27	1			3	1	1		2	1	1	1	4(1)
28-29				1	1	1			1	1	5	1
30-31	2	1							1	2	1	1
32-33	1											
34-35			1							1		
36-37	2											1
38-39	1			1	1				1			
40-41			1		1		1					
42-43										1	3	
44-45	1		1				1	1				
46-47		1		2				1		2	1	1
48-49	1		1	1				1	1	1	1	1
50-51			3		1	1		1	5	3	1	1
52-53	1	2	3	1		2			2	4	3	
54-55	1	1	2			2	1	1	1	1		
56-57	1	2	1		1		2		2		1	
58-59								1	2			
60-61		1	1	3	1	1			1	1		1
62-63				1								

their absence in the spring suggest that some larvae may settle out in less than a year. Conversely, the presence of large larvae (>50 mm) during June, shortly after the end of spawning season (Table 5), suggests that some larvae may be pelagic for over a year, like some Dover sole larvae. Powles and Kohler (1970) believed that *G. cynoglossus* larvae in the North Atlantic are also pelagic for the first year of life.

Petrale sole larvae were only found during 4 mo, March-June (Figure 4). No distinct progression of stages was apparent, though stage I larvae were only collected in March and April and stage IV only in June. Petrale sole spawn in winter and early spring, November to April in the northeastern Pacific (Harry 1959; Porter 1964; Alderdice and Forrester 1971), so our limited data indicate an egg and larval period of about 6 mo.

INSHORE-OFFSHORE AND NORTH-SOUTH DISTRIBUTION

Both Dover and rex sole larvae were widely distributed offshore. All three species of flounders are considered to have "offshore" larvae by Richardson and Pearcy (1977).

Bongo nets collected Dover sole larvae at all but the 6-km station (Table 6), although the larvae were most frequent and abundant at the offshore stations (56-111 km), where 84.8% of all larvae were taken. Peak abundance occurred at the 111-km station. Rex sole were taken at all stations but were more abundant offshore (46-111 km) where 80.5% of all larvae occurred. Peak abundance was at 46 km. One specimen of petrale sole was taken 56 km offshore.

Largest mid-water trawl catches of Dover sole larvae were usually made in oceanic waters more than 46 km offshore along all four station lines (Table 7). Some larvae were taken as far as 550 km offshore. Rex sole larvae were most common at the 28- to 83-km stations over the outer shelf and slope, but were also captured farther offshore. The farthest offshore a rex sole larva was collected was 195 km. Petrale sole larvae were collected from 2 to 120 km from the coast. About half the petrale larvae were caught 83-120 km offshore.

Lengths of larvae at varying distances from the coast provide clues to inshore-offshore dispersal. In the bongo net transect data, Dover sole larvae <11 mm were collected at all stations except 6 km, but the greatest numbers of small larvae were at the 93- and 111-km stations. Larger larvae (11-26 mm) occurred only at stations 56 to 111 km

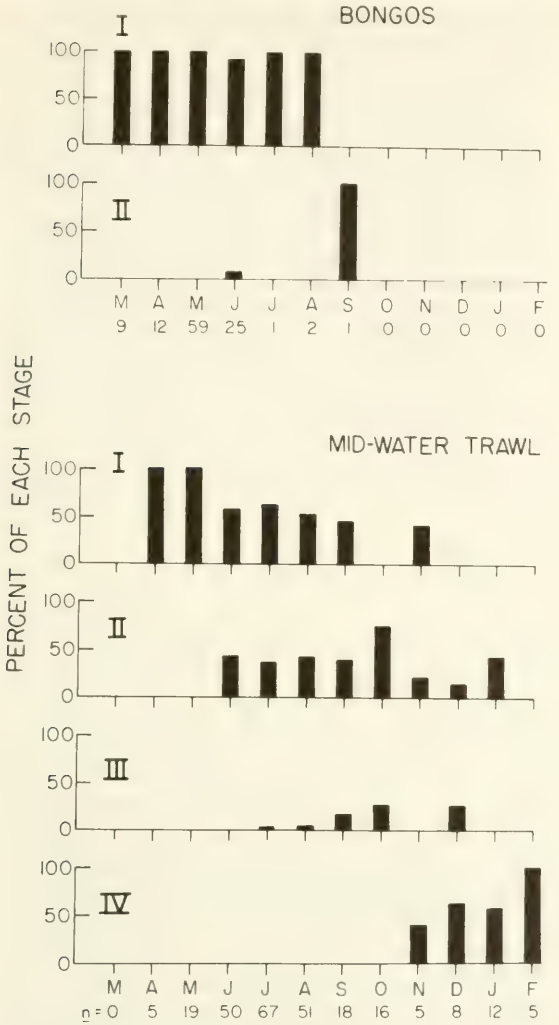

FIGURE 3.—The relative abundance of each stage of rex sole larvae in bongo transect and mid-water trawl collections during all months.

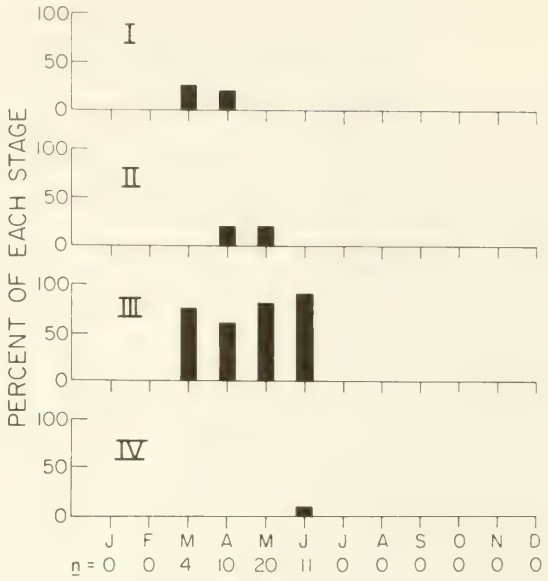

FIGURE 4.—The relative abundance of each stage of petrale sole larvae in bongo transect and mid-water trawl collections during all months.

offshore. Similarly, rex sole larvae <11 mm were taken at all stations but greatest numbers occurred at the 46-km station. All but 2 of the 29 rex sole larvae ≥11 mm (11-67 mm) were taken at stations 37 to 111 km offshore. These trends suggest that larvae >11 mm of both species are most common in waters beyond the continental shelf. In the bongo net grid samples, Dover and rex sole larvae, which were mostly smaller than 10 mm SL, were widely distributed. They were taken at all distances 2 to 56 km from the coast, but always in low numbers. Mean numbers per 10 m² sea surface were less than 0.30 for Dover sole larvae and 0.70 for rex sole larvae.

No obvious trend of increasing mean size of large Dover or rex sole larvae with distance offshore was apparent from mid-water trawl collections. However, the eight rex sole larvae <30 mm SL in mid-water trawl collections were all captured between 9 and 83 km offshore.

In mid-water trawl samples, the ratio of Dover larvae ≤30 mm to those larvae >30 mm during the summer (May-September) was 15:1 and 6:1 at stations inshore and offshore of 83 km, respectively. This indicates a preponderance of "smaller" larvae over the shelf and slope, probably a result of spawning the previous winter. During winter (October-April) these ratios were 1:2 inshore and 2:1 offshore of 83 km, reflecting a greater proportion of large larvae during the winter especially over the shelf and slope where they will settle.

North-south trends were not as obvious. In the bongo grid samples, Dover sole larvae were taken on 9 of the 12 lines with the mean number per 10 m² on each line always less than 0.26. Rex sole larvae were taken on all 12 lines. Mean number per 10 m² on each line ranged from 0.24 to 1.26 with the greatest numbers occurring over Heceta Bank. One petrale sole larva was taken 37 km offshore just north of Cape Blanco. In the mid-water trawl samples the mean catch per tow of Dover sole was about the same along the three northern station lines, and was about twice as

TABLE 5.—Length-frequency distributions of *Glyptocephalus zachirus* larvae collected during various months. Numbers in parentheses denote larvae caught in bongo nets; numbers without parentheses denote larvae caught in mid-water trawls.

Standard Length (mm)	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
4-5	(1)	(4)										
6-7	(3)	(20)	(2)									(3)
8-9	(6)	(28)	(3)									(5)
10-11	(1)	(2)	(1)									
12-13	1	(2)										
14-15		(1)	(1)									
16-17	(1)	(1)	(2)									
18-19	1		1(1)		1							
20-21	1	1	1(1)		1							
22-23		2		1								
24-25	1	1	2(2)	1								
26-27			1(2)	2								
28-29			1	2								
30-31	1	2	2(2)	3								
32-33		1	3	2	2(1)							
34-35			1(1)	4		2						
36-37			3	4	2							
38-39		1	1(1)	5	4	1		1				
40-41		3	1	5	5(1)	2	1		1			
42-43		1	2(1)	6	1	2	2					
44-45		2	(3)	2(1)	3		1	1				
46-47			2	4	4							
48-49		1	1(1)	6	1		1	1				
50-51			2	5	5	1	3			3		
52-53		1	4	4	4		1	2		4	1	
54-55			3(1)	1	1		1		2		4	
56-57		1	1		3	2	1		1	2		
58-59			3	4	3	2	2		3			
60-61			2	1	4	3				1		
62-63			3	2	2	2						
64-65			2	1	4		2			1		
66-67						1(1)						
68-69			3				1					
70-71			3							1		
72-73			1	1					1			
74-75				1								
89					1							

TABLE 6.—Catches of Dover sole and rex sole larvae from bongo net collections taken on the transect off Newport, Oreg., from January 1971 to August 1972. Numbers of larvae in each sample were standardized to number under 10 m^2 sea surface.

Item	Station (kilometers from coast) 2	6	9	18	28	37	46	56	65	74	93	111
No. tows	29	27	30	30	23	25	21	25	18	21	20	18
Frequency of Dover	2	0	2	1	2	1	2	3	2	4	6	7
Mean no. Dover/10 m^2	0.07	0	0.09	0.03	0.11	0.08	0.16	0.34	0.51	0.38	0.95	1.75
Frequency of rex	2	2	4	4	3	3	5	4	3	5	3	3
Mean no. rex/10 m^2	0.03	0.05	0.23	0.15	0.21	0.25	2.27	0.69	0.52	0.55	0.32	0.51

TABLE 7.—Catches of Dover sole and rex sole larvae at various distances from shore. The data are from mid-water trawl collections taken during all seasons of the year, 1961-67, along four transect lines (Figure 1).

Item	Distance offshore (kilometers) 9	28	46	83	120	158-306
Columbia River:						
No. tows	2	15	18	16	12	9
No. Dover (no./tow)	1(0.50)	3(0.20)	4(0.22)	2(0.12)	3(0.25)	5(0.55)
No. rex (no./tow)	0(0)	1(0.07)	3(0.17)	1(0.06)	0(0)	1(0.11)
Newport:						
No. tows	2	53	57	61	62	54
No. Dover (no./tow)	0(0)	1(0.02)	3(0.05)	11(0.18)	40(0.64)	17(0.31)
No. rex (no./tow)	0(0)	11(0.21)	24(0.42)	32(0.52)	9(0.14)	8(0.15)
Coos Bay:						
No. tows	0	15	15	14	6	15
No. Dover (no./tow)	-	2(0.13)	6(0.40)	6(0.42)	1(0.17)	4(0.27)
No. rex (no./tow)	-	7(0.47)	4(0.27)	7(0.50)	0(0)	1(0.07)
Brookings:						
No. tows	7	8	12	12	8	37
No. Dover (no./tow)	0(0)	0(0)	10(0.83)	10(0.83)	2(0.25)	22(0.59)
No. rex (no./tow)	3(0.43)	6(0.75)	9(0.75)	5(0.42)	2(0.25)	7(0.19)

high off Brookings, Oreg. Mean abundance of rex sole larvae was lowest off the Columbia River (Table 7).

Certainly the distribution of these larvae is related to both alongshore and inshore-offshore currents over the continental shelf and slope as well as to spawning location of adults. The predominant flow throughout the year off Oregon is alongshore, yet current reversals occur (south in summer, north in winter) and subsurface countercurrents are present (Huyer et al. 1975). There is additional transport of surface waters offshore in summer, and inshore in winter (Wyatt et al. 1972). Perhaps these interacting current systems serve to maintain the majority of these larvae within areas favorable for settling, even though they have extended pelagic lives and the continental margin off Oregon is narrow.

VERTICAL DISTRIBUTION

Information was obtained on vertical distribution of Dover sole larvae from a series of opening-closing mid-water trawl collections from the upper 1,000 m, 120 km off Newport. There, water depth was about 2,800 m. All but two larvae were found in the upper 600 m, revealing that this species may occupy a broad depth range (Table 8), nearly as extensive as the bathymetric range of adult Dover sole (Alton 1972). Larvae were most abundant (196 larvae/10^5 m^3) in the upper 50 m. Convincing evidence for diel vertical migration was absent, although the vertical distribution of larvae during the July 1971 cruise appeared to be shallower by night than by day. Rae (1953) concluded that *Microstomus kitt* larvae exhibited diel vertical migration of 10-20 m into near-surface waters at night. Such a shallow migration would not be detectable from our samples.

TABLE 8.—Average catches (number/10^5 m^3 water filtered) of *Microstomus pacificus* larvae in an opening-closing mid-water trawl during one cruise in July 1971 and five cruises July 1971-September 1974, 120 km off the central Oregon coast; water depth was 2,800 m. D = day, N = night.

Depth (m)	Total numbers				No. per 10^5 m^3			
	July 1971		1971-74		July 1971		1971-74	
	D	N	D	N	D	N	D	N
0-50	27	15	53	29	188	196	15	4
50-100	6	11	14	13	20	127	6	2
100-150	21	1	21	1	156	5	11	<1
150-200	2	5	4	5	8	52	2	2
200-300	3	1	12	16	6	5	2	4
300-400	0	0	23	9	0	0	2	1
400-500	17	0	31	4	24	0	4	1
500-600	4	0	11	0	7	0	3	0
600-700	0	0	0	0	0	0	0	0
700-800	0	0	0	0	0	0	0	0
800-900	0	0	0	0	0	0	0	0
900-1,000	0	0	0	2	0	0	0	2

BENTHIC JUVENILES

The season and depth of occurrence of the smallest benthic juveniles are important indicators of the lengths of the pelagic phase of these fishes. Hagerman (1952) reported that young Dover sole become demersal between 50 and 55 mm total length (TL). Mearns and Gammon (see footnote 8) caught juvenile Dover sole of 45-75 mm SL during both mid-autumn and early spring off southern California, suggesting two major periods of recruitment. Demory (1971, see footnote 4, and pers. commun.) caught the largest numbers of small juvenile Dover sole (40-70 mm TL) in February in bottom trawls between 130 and 183 m depth off northern Oregon. According to Demory, these fish, which were 1 yr of age, subsequently move into shallow water in the summer. Though not common, we have taken Dover sole of 40-50 mm SL in the winter in beam trawl collections on the outer shelf off central Oregon. These results indicate that Dover sole off Oregon usually complete metamorphosis and take up a benthic life on the outer continental shelf after about 1 yr, when they are less than 50 mm long. Larger larvae are probably older than a year and have delayed complete transformation to the benthic juvenile form. These large, "holdover" larvae may contribute little to the juvenile and subsequent adult age-groups, based on Demory's (1972b for methods, pers. commun.) observation of two circuli patterns in the scales of small juvenile Dover sole. These were: a dominant pattern with 6-9 circuli, and another rarer pattern with 20 or more circuli. Thus fish with the larger number of circuli probably represent our large larvae, which become benthic well after 1 yr.

Juvenile rex sole, 40-60 mm SL, were common in our beam trawl collections on the outer edge of the continental shelf (150-200 m depth) during the winter months off central Oregon. We also collected 22 *G. zachirus* larvae of 46-60 mm TL (stage III) in an otter trawl at 230-260 m depth off Coos Bay, Oreg., in September. We do not know if these rex sole larvae were benthonic before metamorphosis was completed or if they were living pelagically when caught by the trawl. From these data, we surmise that rex sole settle to the bottom mainly on the outer continental shelf during the winter when they are about 1 yr old. It is possible

that they use this area as a nursery during early benthic life as has been suggested for *G. cynoglossus* on the east coast (Powles and Kohler 1970; Markle 1975). Rex sole smaller than and larger than 180 mm TL have broadly overlapping depth ranges off Oregon (Demory 1971), unlike *G. cynoglossus* which occupies distinct depth zones as juveniles and adults (Powles and Kohler 1970).

Juvenile *E. jordani* were uncommon in bottom trawls. Only two small individuals (65 and 83 mm SL) were found in 115 beam trawl collections. We found only 28 small petrale sole (62-107 mm TL), collected in October and November at 64-82 m depth, from extensive otter trawl collections off Newport in 1972. Examination of otoliths indicated these petrale sole were all in their first year of growth. This suggests that metamorphosis of this species occurs during the fall of their first year when they settle to the bottom of the inner continental shelf off Oregon. Our findings are corroborated by those of other researchers. In British Columbia waters, Ketchen and Forrester (1966) found a few 0-age petrale sole only at depths of 18-90 m between May and August. From extensive otter trawl collections off northern California Gregory and Jow (1976) reported 17 petrale sole (60-100 mm TL) in September and October between 28 and 73 m.

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SELECTIVITY OF GILL NETS ON ESTUARINE AND COASTAL FISHES FROM ST. ANDREW BAY, FLORIDA

LEE TRENT AND PAUL J. PRISTAS[1]

ABSTRACT

Eleven gill nets, each of a different mesh size, were fished 126 days from 4 April to 29 December 1973 in St. Andrew Bay, Fla. Of the estuarine and coastal fishes that were caught, 22 were in numbers sufficient to evaluate the relation between length of fish and mesh size. Mean length increased with an increase in mesh size for 20 species. Ten species—gulf menhaden, *Brevoortia patronus;* spot, *Leiostomus xanthurus;* sea catfish, *Arius felis;* pinfish, *Lagodon rhomboides;* Atlantic croaker, *Micropogon undulatus;* blue runner, *Caranx crysos;* pigfish, *Orthopristis chrysoptera;* bluefish, *Pomatomus saltatrix;* Spanish mackerel, *Scomberomorus maculatus;* yellowfin menhaden, *B. smithi*—were caught in sufficient numbers to apply and evaluate the normal probability model to define gill net selectivity. One or more of the three assumptions—normality of selectivity curve, linearity of mean length-mesh size relation, and constancy of standard deviation between mesh sizes—inherent in the model was violated by the data for each species to which the model was applied except Atlantic croaker and blue runner. Useful information was provided, however, in relation to evaluating mesh-size regulations and for determining mesh sizes for increasing capture efficiencies in gill net fisheries.

Rarely will a particular type of fishing gear capture all sizes of a species of fish with equal probability. Gill nets are selective in that, for a particular species and mesh size, fish are retained with high probability at certain lengths and with decreasing probability for larger and smaller individuals. Most streamlined fish without projecting spines, teeth, or opercular bones are caught in gill nets by becoming tightly wedged or enmeshed in the webbing. To describe selectivity for these streamlined fishes, a smooth unimodal curve with capture probabilities descending to zero is suggested by several workers (Regier and Robson 1966). Fish species that are not streamlined, or that have stiff projecting appendages or spines, are frequently caught entangled in the webbing rather than, or in addition to, becoming wedged in the meshes. For these species skewed or multimodal curves are usually necessary to describe capture probabilities (Hamley and Regier 1973).

An understanding of the selection properties of gill nets is necessary to evaluate catch statistics, alter catch per unit effort, and regulate the sizes of caught fish. Most methods of estimating recruitment, growth, sex ratio, and survival of a fish species require samples that are representative of the population in respect to size of individuals. Only if size selectivity of the fishing gear is known can the catch statistics be adjusted and used to provide correct estimates of the parameters of interest (Cucin and Regier 1966). Alternatively, an understanding of how selectivity depends on the characteristics of the gear may be used to design a series of gear to yield samples of known characteristics over a specified size range (Regier and Robson 1966). A knowledge of the size selective properties of the gear permits recommendations of mesh sizes to maximize (increase capture efficiency) or minimize (protect from harvest) the catch on certain sizes and species.

Published information is not available on the lengths of fish caught in particular mesh sizes of gill nets for estuarine and coastal fishes inhabiting the Gulf of Mexico except for a meager amount on two species. Klima (1959) reported length-frequency distributions of Spanish mackerel, *Scomberomorus maculatus,* that were caught in 7.9- and 9.0-cm stretched-mesh gill nets. Modal lengths of those were 37 and 43 cm, respectively. Tabb (1960) reported a length-frequency distribution of spotted seatrout, *Cynoscion nebulosus,* that were caught in 8.0-cm stretched-mesh gill nets. Modal length of the distribution was 33.5 cm.

Mesh sizes of gill nets most frequently used to capture various species of fish in the commercial gill net fishery in Florida were reported by Siebenaler (1955).

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The objectives of this study for each species caught in sufficient abundance were: 1) to show the relations between mesh size and the mean length and standard deviation in length of fish, 2) to define gill net selectivity by applying the normal probability model, 3) to evaluate the applicability of this model for defining selectivity, and 4) to discuss uses of the derived information.

STUDY AREA

The study area was in the St. Andrew Bay system located in northwest Florida along the Gulf of Mexico. This bay system, compared to most other northern gulf estuarine systems, is deep, has high salinities, low freshwater inflows, large areas of submerged marine grasses, low turbidities, high percentages of sand in the substrate, and has fish and crustacean faunas typical of both coastal and estuarine areas (Ichiye and Jones 1961; Hopkins 1966; Brusher and Ogren 1976; May et al. 1976; and Pristas and Trent 1977). The diurnal range of the tide in the St. Andrew Bay system is about 0.5 m.

ASSUMPTIONS

The relation between the mesh size of gill nets and the size of captured fish can be determined by setting a series of gill nets that vary only in respect to mesh size if certain precautions are taken and certain assumptions are valid. Fishing effort must be equal among mesh sizes, i.e., assume all fish of a given length are equally likely to encounter all nets. This means damage to each net must remain low or about equal among mesh sizes, and net locations are equal in respect to the probability of a net catching a particular fish. We must assume that no "gear saturation" occurs, i.e., the number of fish already entangled in the net in no way influences subsequent behavior of other fish and the net, and that no "spill-over" occurs, i.e., large fish do not lead along the nets until they encounter a large enough mesh in which perhaps to become enmeshed or entangled (Regier and Robson 1966). We must further assume that loss of fish from the nets through predation is not dependent on mesh size or the size of fish.

GEAR AND METHODS

Eleven gill nets, each of a different mesh size, were fished for 126 days from 4 April to 29 December 1973 at a location about 400-1,000 m northwest of Courtney Point in St. Andrew Bay. From 4 April through 20 September, the nets were set every 14th day and fished for 72 consecutive hours. From 20 September, the nets were fished continuously until 13 December. The nets were set again on 26 December and fished for 72 h. Nets were anchored about 50 m apart parallel to each other, perpendicular to shore, and in water depths of 2.2 to 2.6 m (mean low tide). Nets were randomized among net location each time the nets were set. During the continuous fishing in the autumn, the nets were randomized among locations twice during each 2-wk period. Net damage to each net was maintained below 10% of the total surface area.

Increments of mesh sizes in the series of fished nets were small, so that widely overlapping ranges of fish lengths would result. Mesh sizes used in this study were chosen to catch the more abundant species frequenting the St. Andrew Bay area (Pristas and Trent 1977). Stretched-mesh sizes ranged from 6.35 cm (2.5 inches) to 12.70 cm (5.0 inches) in 0.63-cm (0.25-inch) increments.

The nets were 33.3 m long and 3.3 m deep. They were made of #208 clear monofilament (0.33 mm diameter, filament break strength about 26.4 kg) nylon webbing. The webbing was hung to the float and leadlines on the half basis (two lengths of stretched webbing to one length of float or leadline, i.e., a hanging coefficient of 0.5).

Fish were removed from the nets between 1 h before and 2 h after sunrise and occasionally between sunset and 1 h after. The total numbers of each species, including damaged specimens, were counted. Lengths of undamaged specimens were measured to the nearest 0.5 cm. Fork length (tip of snout to fork of tail) was measured for those fishes having forked tails and total length (tip of snout horizontally to extremity of the caudal fin) was measured for Atlantic croaker, *Micropogon undulatus*, and sharks.

Length-frequency distributions of the catch by species and mesh size, based on the number of fish that were measured, were adjusted to represent the number of fish that were caught (those measured plus those damaged), so that the number making up each distribution represented catch per unit effort for each net.

MODEL FOR DETERMINING SELECTIVITY

Basic mathematical models, or modifications of

basic models, for describing selectivity of gill nets were proposed by Baranov (as described by McCombie and Fry 1960), Olsen (1959), McCombie and Fry (1960), Gulland and Harding (1961), Ishida (1962), Holt (1963), Regier and Robson (1966), Hamley (1972), and Hamley and Regier (1973). Ten methods of describing selectivity were used by the above authors. Except for the DeLury method described by Hamley (1972), the mathematics and details of application of these methods were discussed by Regier and Robson (1966).

A comprehensive review of gill net selectivity was presented by Hamley (1975). All basic models, applications and shortcomings of these models, and the variety of factors (thickness, materials, and color of net twine, hanging of net, and methods of fishing) that must be considered in determining selectivity were discussed.

The method proposed by Holt (1963) was used to evaluate selectivity on species that were caught in this study. Holt assumed that: 1) the selectivity curve would take the form of a normal frequency distribution; 2) the efficiencies of two nets with different mesh sizes would be similar for fish of their respective mean lengths; and 3) the standard deviations of the distributions for two different mesh sizes would be equal. The equations for evaluating the above assumptions and for describing selectivity have been given by Holt (1963), Regier and Robson (1966), and Hamley (1975).

If Holt's three asssumptions are analyzed and deemed acceptable, points of the selectivity curve for mesh size m_i can be computed by

$$s_{ij} = \exp\left[-\frac{1}{2s_i^2}(l_j - \bar{l}_i)^2\right]$$

where l_j = length of fish in length stratum j
$\bar{l}_i$ = mean selection length
s_i = standard deviation of the selectivity curve
n_{ij} = number of fish of length l_j caught in net m_i.

Then n_{ij}/s_{ij} can be used to estimate abundance of fish for each l_j and therefore, the length-frequency distribution in the fished population can be estimated from the length-frequency distribution obtained from fishing a particular mesh size on the population.

An additional assumption is necessary if catches from a series of nets with different mesh sizes are combined and used to estimate the length-frequency distribution of the fished population. The assumption is that the selectivity curves for all meshes have the same shape (each s_i is an estimate of a common s) and amplitude (each net fishes with equal efficiency on the length at which the net is maximally efficient). This assumption was questioned by Ricker (1947), Ishida (1964), Regier and Robson (1966), and Hamley (1972). The assumption can be tested only if the length-frequency distribution of the fished population is known. Hamley and Regier (1973) tested this assumption on walleye, *Stizostedion vitreum vitreum,* which were tagged prior to being recaptured with gill nets, and found that the shapes and amplitudes of their selectivity curves changed with mesh size. This assumption could not be tested in our study.

Information derived from a selectivity study has various uses depending upon the validity of the mathematical model used to describe selectivity and on the accuracy and precision required. The model can be useful for some purposes even if all the assumptions are not met or even if the model is not the most accurate and precise one for describing the empirical data.

The objective of most selectivity studies has been to determine the most appropriate model for describing gill net selectivity for a single species of fish (Regier and Robson 1966). In this study we have attempted to provide as much information as possible about gill net selectivity on 22 species. To 10 of these we applied a single mathematical model and either accepted or rejected the model in relation to each of several potential applications. By accepting the model we do not infer that it is the most accurate or precise model but that the approximation to the data is sufficiently close and accurate to be useful.

NUMBERS AND MEAN LENGTHS OF FISHES SELECTED FOR ANALYSES

Of the 76 species that were caught in the study area during 1973 (May et al. 1976; Pristas and Trent[2]), 22 species had catches exceeding 100 specimens. Of the 22 species, 15 were commercially important in gill net fisheries in one or more states along the south Atlantic and Gulf of Mexico

[2]Pristas, P. J., and L. Trent. 1976. Seasonal abundance, size, and sex ratio of fishes caught with gill nets in St. Andrew Bay, Florida. (Unpubl. manuscr.)

coasts (National Marine Fisheries Service 1974). Number caught (n_i), number measured (nm_i), mean length ($\bar{Sl}_i$), and standard deviation (Ss_i) of mean length for each of the 22 species by mesh size are shown in Table 1.

The assumption that mean lengths of fish that

TABLE 1.—Number of fish caught (n_i), number measured (nm_i), mean length in centimeters ($\bar{Sl}_i$), and standard deviation of length (Ss_i) by stretched mesh size (m_i) and species.

Species		m_i in centimeters and (inches)										
		6.3 (2.5)	7.0 (2.75)	7.6 (3.0)	8.2 (3.25)	8.9 (3.5)	9.5 (3.75)	10.2 (4.0)	10.8 (4.25)	11.4 (4.5)	12.1 (4.75)	12.7 (5.0)
Gulf menhaden,[1]	n_i	726	897	1,339	845	411	99	14	10	3	9	16
Brevoortia patronus	nm_i	696	830	1,062	787	342	89	14	8	2	6	10
	$\bar{Sl}_i$	17.4	19.7	21.3	22.1	22.9	23.7	22.7	23.3	26.0	21.0	22.0
	Ss_i	1.0	1.4	1.1	1.1	1.3	1.4	2.4	3.2	0.7	1.3	1.5
Spot,[1]	n_i	1,830	1,054	172	27	10	0	1	2	0	0	0
Leiostomus xanthurus	nm_i	1,511	942	162	27	7	0	1	2	0	0	0
	$\bar{Sl}_i$	19.2	20.3	21.6	23.3	23.4	—	18.5	22.7	—	—	—
	Ss_i	0.8	0.8	1.0	1.3	2.1	—	—	0.3	—	—	—
Sea catfish,	n_i	314	393	463	344	303	229	229	154	66	47	37
Arius felis	nm_i	236	323	394	283	258	205	202	136	56	43	33
	$\bar{Sl}_i$	24.8	26.2	27.8	29.4	30.7	32.1	32.7	33.9	33.9	33.5	33.3
	Ss_i	3.4	2.8	2.6	2.7	3.1	3.0	3.3	3.5	4.1	4.6	3.7
Pinfish,	n_i	1,272	617	343	112	88	8	17	14	8	2	2
Lagodon rhomboides	nm_i	1,230	581	315	108	82	7	15	13	8	2	2
	$\bar{Sl}_i$	16.5	16.6	16.9	17.3	16.6	15.8	15.9	17.6	16.6	18.0	17.0
	Ss_i	1.3	1.8	2.1	2.7	2.6	2.3	1.4	2.0	1.6	0.0	0.0
Atlantic croaker,[1]	n_i	731	741	479	134	182	70	24	7	3	1	3
Micropogon undulatus	nm_i	450	602	378	107	155	55	23	7	3	1	3
	$\bar{Sl}_i$	22.6	24.5	26.1	28.5	29.6	31.2	32.5	35.0	32.7	25.0	24.5
	Ss_i	1.3	1.6	1.8	1.6	2.4	2.5	3.2	2.7	5.6	—	11.4
Blue runner,[1]	n_i	439	468	500	140	77	47	58	32	13	4	4
Caranx crysos	nm_i	392	429	477	122	62	46	52	31	12	4	3
	$\bar{Sl}_i$	21.1	22.4	24.5	26.6	29.5	32.5	36.3	37.4	32.6	29.7	27.2
	Ss_i	1.4	1.7	2.1	3.0	4.2	4.3	4.4	3.4	8.4	9.2	11.2
Pigfish,[1]	n_i	617	359	127	36	3	1	2	0	0	2	0
Orthopristis chrysoptera	nm_i	597	346	124	36	3	1	2	0	0	2	0
	$\bar{Sl}_i$	18.1	19.5	21.0	21.8	22.5	24.5	20.0	—	—	17.5	—
	Ss_i	0.7	1.0	0.9	1.3	1.8	—	0.7	—	—	0.7	—
Bluefish,[1]	n_i	148	247	287	164	69	95	46	25	8	11	4
Pomatomus saltratrix	nm_i	138	236	279	148	67	91	46	22	7	11	4
	$\bar{Sl}_i$	30.1	31.9	33.4	36.3	38.7	39.1	41.4	38.9	40.6	35.6	31.0
	Ss_i	3.8	3.8	3.5	3.9	3.4	4.0	3.7	7.1	5.9	11.0	4.4
Spanish mackerel,[1]	n_i	146	109	145	133	101	81	41	27	17	8	5
Scomberomorus maculatus	nm_i	126	91	130	108	81	76	38	26	15	5	5
	$\bar{Sl}_i$	33.4	34.5	36.0	38.1	39.7	42.2	44.5	45.7	47.4	44.6	49.1
	Ss_i	4.9	4.7	4.8	4.9	5.0	4.9	4.2	4.3	7.9	9.1	7.4
Yellowfin menhaden,[1]	n_i	2	4	28	100	224	191	170	49	10	12	1
Brevoortia smithi	nm_i	2	3	28	94	204	182	161	44	10	12	1
	$\bar{Sl}_i$	23.0	24.3	24.4	25.5	25.8	26.5	26.4	26.6	28.5	28.4	31.0
	Ss_i	4.9	0.8	1.2	1.3	1.1	1.1	1.2	1.0	1.7	1.5	—
Gafftopsail catfish,[1]	n_i	2	5	10	14	15	12	7	24	41	50	85
Bagre marinus	nm_i	2	5	10	14	15	12	5	24	41	50	81
	$\bar{Sl}_i$	39.7	43.3	45.1	40.4	41.8	40.2	39.9	41.7	42.9	43.8	44.6
	Ss_i	3.2	1.7	5.3	5.7	5.7	6.5	5.0	4.3	3.9	3.4	4.1
Spotted seatrout,[1]	n_i	77	66	32	26	14	13	11	3	1	1	1
Cynoscion nebulosus	nm_i	70	59	28	22	12	13	11	3	1	1	1
	$\bar{Sl}_i$	30.3	32.7	36.3	38.6	43.7	45.5	47.8	50.7	54.0	57.0	36.5
	Ss_i	2.7	4.1	3.1	3.6	3.6	4.3	3.8	7.2	—	—	—
Crevalle jack,[1]	n_i	64	28	26	17	10	12	18	8	26	23	1
Caranx hippos	nm_i	63	27	26	17	10	12	18	8	26	23	0
	$\bar{Sl}_i$	16.2	18.5	19.0	19.9	29.1	33.8	31.3	22.8	37.2	41.8	—
	Ss_i	0.9	3.0	1.0	5.9	9.3	6.8	3.6	5.6	2.6	10.3	—
Little tunny,	n_i	24	8	25	30	6	6	6	16	23	12	26
Euthynnus alletteratus	nm_i	24	8	25	29	5	6	4	15	23	10	26
	$\bar{Sl}_i$	42.3	51.2	44.6	58.3	58.3	60.5	57.4	59.0	58.8	54.6	57.3
	Ss_i	17.8	12.6	15.8	7.3	1.7	1.8	4.0	3.8	2.4	10.9	8.0
Atlantic sharpnose shark,	n_i	6	15	19	18	15	17	21	15	7	9	7
Rhizoprionodon terraenovae	nm_i	6	11	18	18	14	16	20	14	7	9	7
	$\bar{Sl}_i$	50.4	59.1	61.5	60.0	63.6	65.8	62.6	72.4	72.6	72.1	74.8
	Ss_i	4.1	14.6	10.1	12.2	11.6	13.1	11.9	10.4	6.0	13.3	9.8
Atlantic bumper,	n_i	61	64	17	2	3	1	0	0	2	0	1
Chloroscombrus chrysurus	nm_i	61	63	17	2	3	1	0	0	2	0	1
	$\bar{Sl}_i$	15.0	15.6	15.7	16.5	17.7	17.0	—	—	19.2	—	15.5
	Ss_i	1.2	1.1	1.8	2.8	1.8	—	—	—	4.6	—	—

TABLE 1.—Continued.

Species		m_i in centimeters and (inches) 6.3 (2.5)	7.0 (2.75)	7.6 (3.0)	8.2 (3.25)	8.9 (3.5)	9.5 (3.75)	10.2 (4.0)	10.8 (4.25)	11.4 (4.5)	12.1 (4.75)	12.7 (5.0)
Florida pompano,[1]	n_i	0	2	7	11	14	20	19	18	19	20	18
Trachinotus carolinus	nm_i	0	2	7	10	13	20	19	18	19	20	18
	Sl_i	—	22.2	18.9	19.1	21.0	23.4	25.3	27.6	29.8	31.4	32.4
	Ss_i	—	3.9	1.7	1.5	4.2	3.0	3.9	2.4	2.9	2.1	3.9
Inshore lizardfish,	n_i	60	41	11	4	4	0	3	1	4	1	1
Synodus foetens	nm_i	51	36	11	4	3	0	3	1	4	1	1
	Sl_i	36.1	38.6	39.6	39.5	33.5	—	35.0	26.0	31.2	33.5	38.0
	Ss_i	2.9	2.5	3.0	2.5	5.8	—	6.0	—	2.5	—	—
Gulf flounder,[1]	n_i	3	1	4	1	9	8	16	8	23	25	28
Paralichthys albigutta	nm_i	3	1	4	1	8	8	14	8	23	23	28
	Sl_i	24.8	30.0	25.1	24.5	28.9	28.3	30.9	30.2	32.3	33.9	36.4
	Ss_i	8.3	—	3.3	—	6.1	3.7	4.7	3.3	3.1	4.2	3.8
Bonnethead shark,	n_i	0	3	0	3	10	14	20	11	15	22	29
Sphyrna tiburo	nm_i	0	3	0	3	10	14	20	11	15	22	28
	Sl_i	—	90.0	—	81.8	86.1	89.7	89.1	86.4	84.5	90.2	89.7
	Ss_i	—	13.1	—	11.3	17.0	14.4	10.6	12.8	15.1	7.7	10.0
Ladyfish,[1]	n_i	49	21	17	4	6	1	1	3	4	4	2
Elops saurus	nm_i	36	19	14	2	6	1	1	2	3	3	2
	Sl_i	35.1	42.3	42.8	46.5	41.8	36.5	26.5	47.7	32.8	31.3	38.2
	Ss_i	4.7	5.0	4.4	6.4	2.2	—	—	8.1	11.8	7.9	3.9
Sand seatrout,[1]	n_i	63	14	14	2	3	1	3	0	0	1	1
Cynoscion arenarius	nm_i	49	12	14	2	3	1	2	0	0	1	1
	Sl_i	29.7	32.1	33.5	35.2	31.3	20.0	24.2	—	—	54.0	26.0
	Ss_i	2.9	1.4	5.1	2.5	6.8	—	1.8	—	—	—	—

[1]Caught commercially in gill nets (National Marine Fisheries Service 1974).

are caught in gill nets increase with an increase in mesh size seemed probable at least over part of the range of mesh sizes, for 20 of the 22 species (Figure 1). The two species that did not show a definite increase in mean length with an increase in mesh size were little tunny, *Euthynnus alletteratus,* and bonnethead shark, *Sphyrna tiburo.* Of the 22 species, none was caught (in numbers where $nm_i>9$) in every mesh size. The relation of an increase in mean length for 20 species (little tunny and bonnethead shark excluded) with an increase in mesh size did not hold throughout the range of mesh sizes for gulf menhaden, *Brevoortia patronus;* sea catfish, *Arius felis;* pinfish, *Lagodon rhomboides;* blue runner, *Caranx crysos;* bluefish, *Pomatomus saltatrix;* gafftopsail catfish, *Bagre marinus;* crevalle jack, *Caranx hippos;* Atlantic sharpnose shark, *Rhizoprionodon terraenovae;* and yellowfin menhaden, *Brevoortia smithi.* The primary reason for low catches in some mesh sizes and for length not increasing progressively with increasing mesh size was that the length ranges in the fished populations of many species were not great enough to provide the sizes of fish that many of the mesh sizes would efficiently capture. The two species not showing the expected relation usually were entangled or enmeshed in the webbing in an abnormal manner. Most of the little tunny that were caught were too large to determine mean length-mesh size relations in the mesh

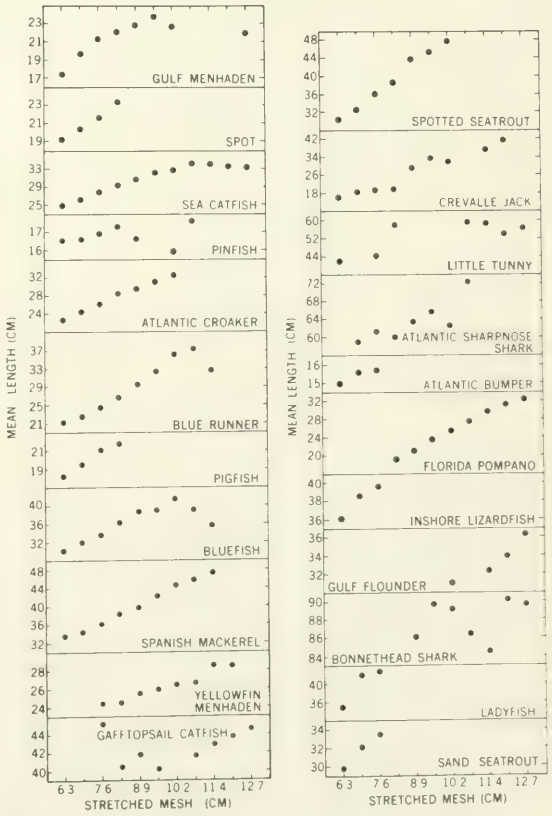

FIGURE 1.—Mean lengths of fishes caught in gill nets of various mesh sizes.

sizes used and were usually caught entangled by their snout and caudal fin; they were rarely wedged in the meshes. Bonnethead sharks were almost always caught in meshes that had been cut (probably by the sharks) and with their teeth entangled in adjacent meshes; because of these circumstances we did not expect a correlation between the size of shark and mesh size.

Based on the data requirements of Holt's method, only the 10 most abundant species (Table 1) were selected to evaluate one or more of the three assumptions—normality of selection curve, linearity of mean length-mesh size relation, and constancy of standard deviation between mesh sizes—required for Holt's model. For these species, length-frequency distributions for those mesh sizes where $n_i > 50$ are shown in Appendix Tables 1-3. These distributions are provided as the basis for our evaluation of selectivity and for applying other mathematical models to the data if other investigators so desire.

SPECIES CAUGHT IN GREATEST ABUNDANCE

Normality of Selection Curves

Natural logarithms of the ratios ($\ln R_{i+1,i,j}$) of numbers of fish of length l_j caught in meshes m_{i+1} and m_i were plotted against lengths of fishes to test normality of the selection curves. Least squares regression equations were computed, and the intercepts (a) and slopes (b) of these equations are shown in Table 2.

Best fits of the points to the straight lines were obtained for spot, *Leiostomus xanthurus;* pigfish, *Orthopristis chrysoptera;* Atlantic croaker; and blue runner. The mean values of $s_{y.x}$ [standard deviation of Y (ratio) for fixed X (length) in linear regression analysis (Steel and Torrie 1960)] were lowest for these four species and ranged from 0.211 to 0.319 (Table 2). Slight curvilinearity appeared, however, in the data for the 7.0/6.3 and 7.6/7.0 cm

TABLE 2.—Coefficients of, and estimates from, least squares regression equations of $\ln R_{i+1,i,j}$ on length by species and mesh-size pair, and k values by species.

Species	Stretched-mesh size (cm) (m_i)	a	b	$s_{y.x}$	Calculated mean selection length (l_j in cm)	Standard deviation of selection curve (s_i)
Gulf menhaden	6.3				17.52	
	7.0/6.3	−27.87	1.51	0.512		1.08
	7.0				19.27	
	7.6/7.0	−25.75	1.25	0.669		1.17
	7.6				21.02	
	8.2/7.6	−20.27	0.90	0.259		1.38
	8.2				22.78	
	8.9/8.2	−17.28	0.73	0.146		1.55
	8.9				24.53	
	9.5/8.9	−29.41	1.20	0.303		1.23
	9.5				26.28	
		Mean $s_{y.x}$ = 0.377			k = 2.759	
Spot	6.3				19.20	
	7.0/6.3	−32.27	1.60	0.337		1.10
	7.0				21.12	
	7.6/7.0	−34.28	1.55	0.302		1.11
	7.6				23.05	
		Mean $s_{y.x}$ = 0.319			k = 3.024	
Sea catfish	6.3				22.52	
	7.0/6.3	− 9.62	0.38	0.917		2.36
	7.0				24.77	
	7.6/7.0	− 6.45	0.24	0.840		3.01
	7.6				27.03	
	8.2/7.6	8.64	0.29	0.042		2.71
	8.2				29.28	
	8.9/8.2	− 8.09	0.26	0.354		2.91
	8.9				31.53	
	9.5/8.9	−10.40	0.32	0.202		2.66
	9.5				33.78	
	10.2/9.5	− 5.65	0.17	0.260		3.73
	10.2				36.03	
	10.8/10.2	− 6.62	0.18	0.151		3.55
	10.8				38.28	
		Mean $s_{y.x}$ = 0.395			k = 3.546	
Pinfish	6.3				19.03	
	7.0/6.3	− 3.30	0.16	0.607		3.40
	7.0				20.94	
	7.6/7.0	− 2.76	0.13	0.281		3.86
	7.6				22.84	
		Mean $s_{y.x}$ = 0.444			k = 2.997	

TABLE 2.—Continued.

Species	Stretched-mesh size (cm) (m_i)	a	b	$s_{y.x}$	Calculated mean selection length ($\hat{l}_i$ in cm)	Standard deviation of selection curve (s_i)
Atlantic croaker	6.3				22.40	
	7.0/6.3	−23.48	1.00	0.296		1.50
	7.0				24.64	
	7.6/7.0	−18.58	0.72	0.312		1.76
	7.6				26.88	
	8.2/7.6	−41.74	1.50	0.335		1.22
	8.2				29.12	
		Mean $s_{y.x}$ = 0.314			k = 3.527	
Blue runner	6.3				20.94	
	7.0/6.3	−16.18	0.74	0.153		1.69
	7.0				23.03	
	7.6/7.0	−22.80	0.97	0.541		1.49
	7.6				25.12	
	8.2/7.6	−18.84	0.70	0.186		1.71
	8.2				27.22	
		Mean $s_{y.x}$ = 0.293			k = 3.297	
Pigfish	6.3				18.09	
	7.0/6.3	−33.77	1.78	0.305		1.01
	7.0				19.90	
	7.6/7.0	−46.96	2.26	0.117		0.89
	7.6				21.71	
		Mean $s_{y.x}$ = 0.211			k = 2.849	
Bluefish	6.3				28.54	
	7.0/6.3	− 2.94	0.11	0.198		5.39
	7.0				31.39	
	7.6/7.0	− 7.27	0.22	0.582		3.59
	7.6				34.25	
	8.2/7.6	− 7.94	0.21	0.312		3.58
	8.2				37.10	
	8.9/8.2	− 9.81	0.24	0.422		3.35
	8.9				39.96	
		Mean $s_{y.x}$ 0.378			k = 4.495	
Spanish mackerel	6.3				30.84	
	7.0/6.3	− 3.25	0.09	0.404		5.54
	7.0				33.92	
	7.6/7.0	− 1.89	0.06	0.673		7.60
	7.6				37.00	
	8.2/7.6	− 4.01	0.11	0.316		5.45
	8.2				40.09	
	8.9/8.2	− 1.36	0.03	0.586		9.71
	8.9				43.17	
	9.5/8.9	− 5.61	0.13	0.436		4.96
	9.5				46.26	
		Mean $s_{y.x}$ = 0.483			k = 4.856	
Yellowfin menhaden	8.2				24.58	
	8.9/8.2	−16.13	0.67	0.427		1.73
	8.9				26.47	
	9.5/8.9	− 8.32	0.31	0.228		2.50
	9.5				28.36	
	10.2/9.5	−13.00	0.49	0.335		2.06
	10.2				30.25	
		Mean $s_{y.x}$ = 0.330			k = 2.978	

mesh-size pairs for blue runner and in the 7.6/7.0 cm mesh-size pair for Atlantic croaker. Spot, pigfish, and Atlantic croaker were almost always caught wedged tightly in the meshes of gill nets. Blue runner were also usually caught in this manner. Occasionally, however, blue runner were caught by the dorsal antrorse spine which hooks over one or more bars of the mesh or meshes. If the spine were not present, these fish could pass through the meshes. Blue runner caught in this manner probably contributed greatly to the variation about regression.

Acceptable fits of the data, at least for most mesh-size pairs, were obtained for gulf and yellowfin menhaden. The normal curve, although acceptable, did not appear to be the most appropriate model to describe selectivity for gulf and yellowfin menhaden because of observed curvilinearity. Values of $s_{y.x}$ were smallest for gulf menhaden in the mesh-size pairs (8.2/7.6, 8.9/8.2 cm; Table 2) that did not exhibit strong curvilinearity. Gulf and yellowfin menhaden were usually caught tightly wedged in the meshes at or near maximum girth, but occasionally the larger individuals taken from a particular mesh size were caught loosely in a mesh by the opercle or preopercle. The slight positive skews observed in the length-frequency distributions (Appendix

Tables 1, 2) for two of the smallest mesh sizes for gulf menhaden and all mesh sizes for yellowfin menhaden probably resulted from fish that were caught by the opercles. This in turn probably accounts for the curvilinearity of the data observed for the two species of menhadens. A cubic exponential equation such as that proposed by Olsen (1959) might more accurately and precisely define selectivity for gulf and yellowfin menhaden over part of the length range of the selectivity curve.

The normal curve also provided acceptable approximations to the data for sea catfish and bluefish, although refinements in data collection procedures, indicating how each fish was caught, are needed to evaluate more accurately the model. Sea catfish are frequently caught entangled by the pectoral and dorsal spines, and bluefish are frequently caught enmeshed or entangled by their teeth, maxillaries, preopercles, and opercles.

The normal curve did not provide acceptable approximations to the data for pinfish and Spanish mackerel. Pinfish were usually caught dorsally by the dorsal antrorse spine and ventrally between a point perpendicular to the antrorse spine and the posterior end of the anal fin. With the fish and webbing interacting in this fashion, the probability of a given size of pinfish being caught was probably about equal in a small range of mesh sizes. The girth of a Spanish mackerel increases gradually from its snout to the anterior point of its second dorsal fin. Most individuals are caught wedged in the mesh at any point between just behind the opercle and the point of maximum girth. The point of retention, therefore, is dependent upon the mesh size within a small range of mesh sizes. Also, many are entangled by the teeth, maxillaries, and occasionally by the tail.

Attempts to suggest models which might better define selectivity for sea catfish, bluefish, pinfish, and Spanish mackerel were not made in this study, because the position at which each fish was wedged in the net and—for those fish not wedged in the net—the position at which each fish was entangled was not recorded, and additional catches of bluefish and Spanish mackerel were needed. Holt (1963) suggested that, for species that are caught at two or more distinct positions along their body, selectivity could be defined by regarding the selection curve as the algebraic sum of two or more normal selection curves, or by fitting an empirical curve such as the cubic exponential. Hamley and Regier (1973) found that the selectivity curve for walleyes was bimodal; they resolved this curve into two unimodal components representing fish that were caught by wedging and entangling.

Mean Length-Mesh Size Relation

The second assumption of Holt's method is that mean length of captured fish is proportional to mesh size. To test this assumption, $-2a/b$ was plotted against the sum of mesh sizes ($m_{i+1} + m_i$) for each mesh-size pair (data from Table 2) and for the seven species for which data for at least three mesh-size pairs were available (Figure 2). Mean selection length (a/b or $\bar{l}_i$) in relation to mesh size can also be determined from Figure 2 using the bottom and right-hand scales. Data for Spanish mackerel were plotted even though the assumption of normality (previous section) for this species was rejected. The straight lines in Figure 2 were fitted through the origin by the least squares method and the slopes (k) of these lines are given in Table 2. With k determined, the mean selection length ($\bar{l}_i$) for any mesh size is determined by $\bar{l}_i = m_i k$.

Best fits of the data were obtained for Atlantic croaker, blue runner, and yellowfin menhaden, and acceptable fits were obtained for gulf menhaden and sea catfish. More data are required, however, to determine the degree of fit for the remaining five species (bluefish, Spanish mackerel, and the three species not shown in Figure 2). Although the degree of fit cannot be evaluated for the five species, information presented in Figure 2 or Table 2 can be used to provide rough estimates of mean selection length in relation to mesh size for bluefish, pinfish, spot, pigfish, and Spanish mackerel. Much of the deviation about the regression for bluefish (and possibly sea catfish) probably resulted from fitting the line through the origin (Figure 2). Apparently the mesh size-mean length relation is not linear throughout a range of mesh sizes between 0 and 8.6 cm for bluefish. A more reasonable approximation of the mean length-mesh size relation for bluefish might result by fitting a regular linear regression equation ($Y = a + bX$ rather than $Y = bX$) to the points in Figure 2. For pinfish, spot, and pigfish, rough approximations of the mean length-mesh size relations can be obtained using the k value (Table 2) even though each k was based on only two points and the origin. Variability about regression was great for Spanish mackerel but this information

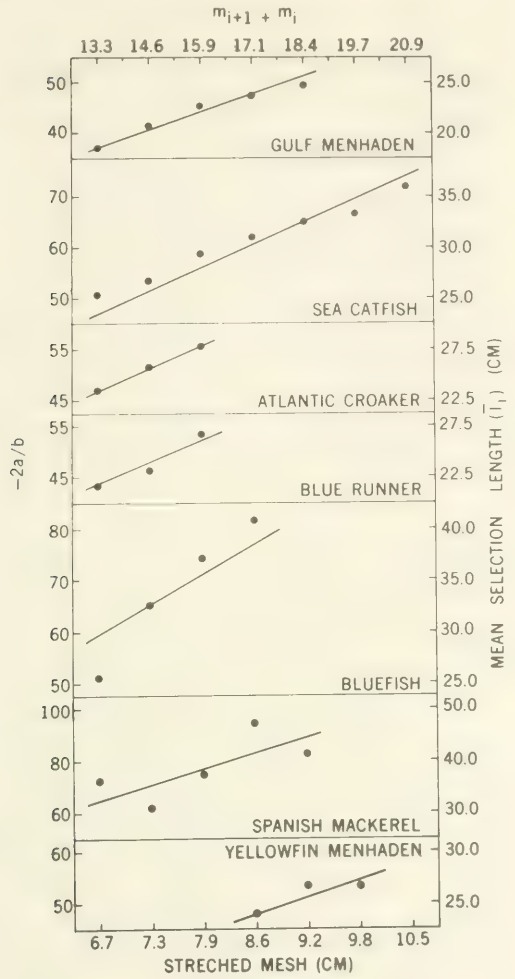

FIGURE 2.—Regression of $-2a/b$ on the sum of mesh sizes ($m_{i+1} + m_i$) and estimates of mean selection length by mesh size for seven species of fishes.

was the best available to estimate the mean length-mesh size relation.

Standard Deviation-Mesh Size Relation

The third assumption of Holt's method is that the standard deviations of length between mesh sizes estimate a common standard deviation. Standard deviations for the selectivity curves are shown in Table 2 by species and mesh-size pair. Standard deviations tended to: increase with an increase in mesh size for gulf menhaden, sea catfish, and Spanish mackerel; decrease with an increase in mesh size for bluefish; and show no apparent trend in relation to mesh size for Atlantic croaker, blue runner, and yellowfin menhaden. Although only two estimates were available for each species, standard deviations appeared similar between mesh-size pairs for spot and pigfish and increased with an increase in mesh size for pinfish.

Standard deviations were much smaller for the species that were usually wedged in the meshes (gulf menhaden, spot, Atlantic croaker, blue runner, pigfish, and yellowfin menhaden) than for those species that were frequently entangled in the meshes or caught at different girths along the body (sea catfish, pinfish, bluefish, and Spanish mackerel).

SPECIES CAUGHT IN LESSER ABUNDANCE

Twelve other species were caught in sufficient numbers to warrant general comments (Table 1, Figure 1). Florida pompano, *Trachinotus carolinus;* spotted seatrout; inshore lizardfish, *Synodus foetens;* ladyfish, *Elops saurus;* and sand seatrout, *Cynoscion arenarius,* usually were enmeshed in the webbing near their maximum girth, although the latter four species sometimes were entangled by their teeth; gulf flounder, *Paralichthys albigutta,* usually were enmeshed just behind the opercle; crevalle jack and Atlantic bumper, *Chloroscombrus chrysurus,* usually were enmeshed but frequently were restricted by the antrorse spine as described for blue runner; gafftopsail catfish usually were enmeshed in the larger mesh sizes but often were entangled by pectoral and dorsal spines in the smaller mesh sizes; little tunny and Atlantic sharpnose and bonnethead sharks usually were entangled in the webbing by their teeth and fins. In general, the magnitude of the standard deviations reflects the amount of entanglement. Standard deviations were lowest for those species normally caught wedged in the meshes and highest for those that were frequently caught entangled (Table 1).

Three of the above-mentioned species—spotted seatrout, Florida pompano, and sand seatrout—are important in the gill net fisheries along the Gulf of Mexico. Although selectivity was not evaluated for these species, owing to insufficient data, estimates of the mean length-mesh size relation can be made from the data in Figure 1. The mean length plotted in Figure 1 would unbiasedly estimate this relation only if equal numbers of fish of each length class and species

were available in the fished population—an assumption that is not valid. Based on the low standard deviations in length for each mesh size (Table 1), however, it appears that a particular mesh size would efficiently capture any of these three species only over narrow length ranges. When this situation exists, only a small amount of bias in the mean length-mesh size relation results from using the estimates derived by plotting the empirical data.

DISCUSSION

Information presented in this paper can be used in fisheries management and research, and by commercial fishermen, in the following ways. We categorized the uses into two types: mesh-size regulations and capture efficiency.

Mesh-Size Regulations

Mesh-size regulations in a fishery should serve specific purposes. These regulations can be useful in controlling the size of captured individuals for some species but not others, depending upon the range in lengths of fish that a given mesh size captures with high efficiency. For species where the regulation can be useful (as indicated by low values of Ss_i or s_i), the objective of the regulation is usually to protect from harvest individuals of a species below a certain length without decreasing efficiency in the commercial gill net fishery. Determination of the smallest mesh size that can be fished is critical for the fish population and for the fishermen. If the mesh size is too small, a significant portion of the small individuals which are to be protected will be caught. If the mesh size is too large, the fishermen will possibly be prevented from using a mesh size which would result in high capture efficiency on legal-sized fish in the population. Information presented in Tables 1 and 2 and Figures 1 and 2 can be used, with various degrees of reliability, to evaluate the usefulness of mesh-size regulations and, for some of the 22 species, to estimate the mesh size which would best fulfill the above stated objective.

At least small amounts of gill net selectivity information were provided on 15 species (Table 1) of fish that were caught and sold by commercial fishermen along the south Atlantic and Gulf of Mexico. The probability that the size composition of the populations for some of these species will eventually be controlled, partially by mesh-size regulations, is high. Of the 15 species, the sizes of individuals caught by gill nets can be controlled, possibly to a degree required for management purposes, by mesh-size regulations, except for bluefish and Spanish mackerel, based on the available data. The degree of control, and the effect that a particular regulation would have on capture efficiency for legal-sized fish in the fishery, can be estimated from values of Ss_i or s_i.

Assuming that a mesh-size regulation is desirable to manage a particular fishery, the steps in estimating the "optimum" mesh size are as follows for two examples—Atlantic croaker and Florida pompano. These two species were selected as examples because, for croaker, data were sufficient to derive selectivity curves and, for pompano, we had insufficient data to derive the curves.

1. Based on management objectives, determine the maximum length (L) of fish which you want to protect from harvest (minimum length of fish to be harvested) and the percent of catch allowed below this length. We arbitrarily selected a length of 20 cm, and <2.5% as the maximum percent allowable of fish below 20 cm, for each species.

2. For Atlantic croaker, the slope (k) for the equation relating mesh size (m_i) and mean selection length ($\bar{l}_i$), and a weighted mean of the s_i estimates of the selectivity curves (Table 2) were used to determine an estimate of the required mesh size. The calculations follow:

A. determine $s = \sqrt{\Sigma(n_i + n_{i+1})s_i^2/\Sigma n_i} = 1.56$

B. determine the minimum mesh size (mm_i)
$mm_i = (L + 2s)/k = (20 \text{ cm} + 3.11)/3.527 = 6.5 \text{ cm}$.

Based on the above, one would expect about 2.5% of the total catch to be composed of Atlantic croaker under 20 cm total length by a gill net having a stretched-mesh size of 6.5 cm.

3. For Florida pompano, appropriate equations to determine $\bar{l}_i$ and s_i are not available, because selection curves could not be determined. These values can be estimated, however, if we assume that the empirical means and standard deviations ($S\bar{l}_i$ and Ss_i; Table 1) are reasonable estimates of $\bar{l}_i$ and s_i. Estimates of the mean length-mesh size relation and standard deviations based on the above assumption would probably yield reasonable and useful approximations for Florida pompano, because: A) the length range within which the pompano were caught efficiently in a

particular mesh size was narrow; B) they rarely became entangled in the webbing; and C) a wide range of sizes was available in the fished population (Table 1). Based on the above assumption, the equations are:

A. $Ss = \Sigma n_i Ss_i^2 / \Sigma n_i = 3.12$
based on data where $n_i > 9$ and
B. $mm_i = (L + 2Ss)/Sk = (20 \text{ cm} + 6.24)/2.517$
$= 10.4$ cm

where Sk = the slope of the least squares regression line fitted through the origin to the points shown in Figure 1 for Florida pompano. Thus, 2.5% of the catch of pompano in gill nets with mesh size of 10.4 cm can be expected to be below 20 cm in length.

Capture Efficiency

Several factors should be considered in the selection of mesh sizes for maximizing the efficiency of capture. Efficiency of capture is defined, or measured by, the dollar return per unit of effort in a gill net fishery. In a gill net fishery the more important factors include: 1) whether individuals of a single species or a group of species are sought; 2) the regulations (mesh size, minimum size limit, etc.) that exist in the fishery; 3) how the gill net is to be fished (anchored, drift, run-around, etc.); 4) values of the species sought and values of various-sized individuals in the fished populations; 5) information on the life history of each species sought, especially the mean length of each age class, the variation in year-class strength between years, and the length-weight relation; 6) the ability, in terms of cost, to use nets with more than one mesh size; and 7) the most efficient mesh sizes for capturing various lengths of fish in the fished population. For this discussion the only factor to be considered is the determination of efficient mesh sizes.

For the 15 species of fish of commercial importance shown in Table 1, the efficiency of capturing a particular length group with maximum efficiency is highly dependent on mesh size for all except bluefish and Spanish mackerel. The range in lengths of fish that a particular mesh size would capture with high efficiency can be estimated from values of s_i or Ss_i given in Tables 1 and 2. The equations,

$$m_i = \frac{\bar{l}_i}{k} \text{ or } m_i = \frac{S\bar{l}_i}{Sk}$$

similar to those in the previous section, and with the same reservations regarding the accuracy of the estimates, can be used to estimate the most efficient mesh sizes for capturing various lengths of fish. A discussion of this type of application in a particular fishery was given by Trent and Hassler (1968).

Limitations on Uses

Selectivity information derived for the 10 species in this study as shown in Figure 1 should be used cautiously, if at all, in adjusting length-frequency distributions. The assumption that the shapes and amplitudes of the selectivity curves are the same for a species could not be tested, but is probably not valid (Hamley and Regier 1973). Further, for all species except Atlantic croaker and blue runner to which we have applied Holt's method, one or more of the three assumptions were invalid, or questionable, or sufficient data were not available to evaluate the assumptions.

Several other factors, not investigated in this study, should be considered when applying our results to estimate mesh sizes for controlling capture efficiency or in adjusting length-frequency distributions of the catch. Selection is dependent to some extent on factors other than mesh size. We used set gill nets, all of which were constructed in the same manner from one type of webbing material. Fishing often occurs with gill nets by encircling the schools or by blocking an area and scaring the fish into the net, or waiting until falling tides force the fish from the blocked area. When fishing is conducted in these ways, many individuals are often caught loosely wedged (Garrod 1961) or loosely entangled in the net; most of these fish, if set gill nets had been used, would have eventually escaped. Selection (size of captured individuals, or efficiency of capture, or both) is also dependent on other factors: natural or synthetic webbing (Washington 1973); color of webbing (Jester 1973); twine size (Hansen 1974); and the hanging coefficient (Hamley 1975).

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APPENDIX TABLE 1.—Length-frequency distributions by mesh size for Gulf menhaden, spot, pinfish, and pigfish.

Length midpoint (cm)	Stretched mesh size in centimeters and (inches)								
	6.3 (2.5)	7.0 (2.75)	7.6 (3.0)	8.2 (3.25)	8.9 (3.5)	9.5 (3.75)	6.3 (2.5)	7.0 (2.75)	7.6 (3.0)
	n_{ij}								
	Gulf menhaden						Spot		
14.0	1.0								
14.5	1.0								
15.0	4.2								
15.5	7.3								
16.0	60.5	1.1	1.3	1.1					
16.5	86.6	3.2					3.6		
17.0	201.3	19.5	2.5	2.1		1.1	17.0		
17.5	134.5	43.2		2.1			44.8		
18.0	110.6	76.7	1.3	1.1			187.7	4.5	
18.5	43.8	87.5	3.8	1.1		1.1	288.2	15.7	1.1
19.0	35.5	121.0	21.4	1.1	2.4		491.7	81.7	1.1
19.5	17.7	127.5	41.6	2.1	2.4		370.6	149.9	2.1
20.0	11.5	128.6	114.7	9.7	3.6		256.8	277.5	10.6
20.5	10.4	85.4	163.9	24.7	7.2	1.1	105.4	211.5	17.0
21.0		84.3	273.6	92.3	13.2	1.1	41.2	176.8	27.6
21.5		44.3	249.6	148.2	34.9	2.2	18.2	83.9	30.8
22.0		32.4	230.7	189.0	66.1	4.4	4.8	33.6	43.5
22.5		25.9	128.6	168.6	66.1	5.6		11.2	21.2
23.0		6.5	64.3	97.7	63.7	8.9		6.7	9.6

APPENDIX TABLE 1.—Continued.

Length midpoint (cm)	Stretched mesh size in centimeters and (inches)								
	6.3 (2.5)	7.0 (2.75)	7.6 (3.0)	8.2 (3.25)	8.9 (3.5)	9.5 (3.75)	6.3 (2.5)	7.0 (2.75)	7.6 (3.0)
	n_{ij}								
	Gulf menhaden						Spot		
23.5		5.4	26.5	52.6	62.5	15.6		1.1	4.2
24.0		1.1	5.0	26.8	32.4	25.6			3.2
24.5		2.2	8.8	16.1	26.4	11.1			
25.0				5.4	14.4	10.0			
25.5		1.1		2.1	8.4	10.0			
26.0				1.1	2.4				
26.5			1.3		2.4	1.1			
27.0					1.2				
27.5					1.2				
	Pinfish						Pigfish		
8.0					1.1				
9.0		1.1							
9.5		1.1							
10.0		1.1							
11.0	1.0		1.1	1.0					
11.5	3.1	4.2			1.1				
12.0	7.2	4.2	1.1						
12.5	2.1	3.2	1.1	1.0					
13.0	5.2	4.2	6.5		4.3				
13.5	23.8	12.7	5.4	1.0	2.1				
14.0	43.4	21.2	10.9	1.0	4.3				
14.5	51.7	18.0	20.7	8.3	4.3		1.0		
15.0	91.0	63.7	21.8	9.3	5.4				
15.5	90.0	51.0	28.3	11.4	10.7		1.0		
16.0	139.6	82.8	33.8	7.2	7.5		3.1		
16.5	194.4	48.8	39.2	13.5	8.6		12.4	1.0	
17.0	264.7	70.1	37.0	10.4	7.5		66.1	3.1	
17.5	167.5	52.0	35.9	12.4	6.4		109.6	6.2	
18.0	124.1	59.5	29.4	11.4	3.2		186.0	24.9	3.1
18.5	30.0	38.2	6.5	6.2	6.4		132.3	42.5	1.0
19.0	23.8	45.7	5.4	1.0	4.3		71.3	70.6	
19.5	2.1	24.4	22.9		2.1		24.8	71.6	4.1
20.0	4.1	6.4	9.8	3.1	1.1		8.3	58.1	8.2
20.5	3.1	1.1	9.8	2.1	2.1		1.0	46.7	23.6
21.0		2.1	9.8	1.0	2.1			24.9	39.9
21.5			2.2	2.1				6.2	24.6
22.0			1.1	2.1				2.1	10.2
22.5			1.1	1.0				1.0	9.2
23.0			2.2		2.1				2.0
23.5				2.1					1.0
24.0					1.1				
26.0				1.0					
26.5				1.0					
29.0				1.0					

APPENDIX TABLE 2.—Length-frequency distributions by mesh size for sea catfish and yellowfin menhaden.

Length midpoint (cm)	Stretched mesh size in centimeters and (inches)								
	6.3 (2.5)	7.0 (2.75)	7.6 (3.0)	8.2 (3.25)	8.9 (3.5)	9.5 (3.75)	10.2 (4.0)	10.8 (4.25)	11.4 (4.5)
	n_{ij}								
	Sea catfish								
14.0	1.3								
16.5	2.6					1.1	2.2	1.1	
19.0	2.6		1.2				1.1	1.1	1.2
21.5	75.8	8.5	2.4	1.2	2.4	1.1			1.2
24.0	127.7	171.5	52.9	10.9	3.6	2.2	5.7	1.1	2.4
26.5	57.2	130.2	182.1	78.0	18.8	5.5	2.2	2.2	1.2
29.0	19.9	43.8	162.1	136.5	119.8	36.9	15.9	6.7	1.2
31.5	17.3	26.9	44.8	85.2	110.4	97.1	77.0	36.4	6.0
34.0	5.4	8.4	14.1	20.6	38.7	59.3	89.5	55.8	26.0
36.5	2.6	3.6	1.2	12.0	5.8	21.3	30.6	36.4	22.4
39.0	1.3		2.4			2.2	3.4	11.4	3.5
41.5						1.1	1.1	1.1	1.2
44.0					1.2	1.1		1.1	
46.5					1.2				
54.0					1.2				
	Yellowfin menhaden								
22.0				6.4					
23.5				39.4	25.3	8.3	4.2		
25.0				38.3	114.2	92.4	37.9		
26.5				14.9	72.5	72.3	92.9		
28.0				1.1	12.1	17.8	31.7		
29.5							2.1		
31.0							1.1		

APPENDIX TABLE 3.—Length-frequency distribution by mesh size for Atlantic croaker, bluefish, Spanish mackerel, and blue runner.

Length midpoint (cm)	Stretched mesh size in centimeters and (inches) 6.3 (2.5)	7.0 (2.75)	7.6 (3.0)	8.2 (3.25)	8.9 (3.5)	9.5 (3.75)
			n_{ij}			
			Atlantic croaker			
19.0	1.6					
19.5	1.6	1.2	1.3			
20.0	16.2	1.2			1.2	
20.5	37.5	2.5				
21.0	61.7	4.9				1.3
21.5	56.8	9.8	1.3			
22.0	125.0	17.2				
22.5	94.2	44.4	5.1			
23.0	116.9	70.2	5.1			
23.5	66.6	81.3	19.0			1.3
24.0	78.0	104.7	31.7			
24.5	27.6	104.7	36.7	0.6	1.2	
25.0	27.6	80.1	58.3	0.6	1.2	
25.5	9.7	64.1	57.0	2.3	1.2	
26.0	3.2	48.0	60.8	4.3	1.2	
26.5	3.2	35.7	53.2	4.9	7.0	
27.0	1.6	29.6	45.6	12.7	14.1	
27.5		16.0	25.3	17.4	12.9	
28.0	1.6	16.0	22.8	25.2	15.3	1.3
28.5		4.9	20.3	13.0	14.1	2.5
29.0		1.2	10.1	20.3	15.3	1.3
29.5		2.5	13.9	10.1	18.8	6.4
30.0			1.3	4.1	12.9	6.4
30.5		1.2	2.5	3.2	15.3	5.1
31.0			2.5	4.6	5.9	7.6
31.5				3.8	11.7	10.2
32.0			2.5	3.8	3.5	3.8
32.5			1.3	1.3	10.6	8.9
33.0				1.7	7.0	5.1
33.5					2.3	1.3
34.0					3.5	2.5
34.5					1.2	
35.0			1.3		3.5	2.5
35.5					1.2	
36.5						2.5
			Bluefish			
24.0	12.8	1.0				
26.5	23.5	24.1	3.0			1.0
29.0	51.5	75.4	68.0	15.4	1.0	3.0
31.5	31.0	61.7	53.4	15.4	3.0	4.0
34.0	10.8	36.6	78.3	26.6	7.2	4.1
36.5	10.7	30.2	52.4	45.5	10.3	13.8
39.0	6.5	6.2	21.6	41.0	24.8	32.8
41.5	1.1	10.4	9.0	12.1	17.5	21.1
44.0		1.0	1.0	6.6	4.1	11.6
46.5				1.1	1.0	4.0
			Spanish mackerel			
26.5	4.6	3.6			1.2	
29.0	42.9	21.6	12.2	2.4		
31.5	37.1	21.6	22.3	13.6	2.4	1.1
34.0	12.7	16.8	39.0	21.0	15.0	2.2
36.5	20.7	13.2	30.2	38.2	18.9	7.5
39.0	13.8	20.4	16.6	14.8	25.2	21.4
41.5	7.0	7.2	12.2	22.2	11.2	17.1
44.0	2.4	3.6	2.2	13.6	13.8	13.9
46.5	3.6	1.2	6.6	3.6	7.5	9.7
49.0	1.2		2.2	1.2	2.4	4.3
51.5					2.4	1.1
54.0			1.1	1.2	1.2	1.1
56.5						1.1
59.0				1.2		1.1

Length midpoint (cm)	Stretched mesh size in centimeters and (inches) 6.3 (2.5)	7.0 (2.75)	7.6 (3.0)	8.2 (3.25)	8.9 (3.5)	9.5 (3.75)
			n_{ij}			
			Blue runner			
16.5	1.1					
17.5	4.5	1.1				
18.0	4.5	1.1				
18.5	6.7					
19.0	13.4	2.2	1.0			
19.5	23.5	5.4				
20.0	63.8	16.4	2.1			
20.5	65.0	13.1				
21.0	82.9	50.2	5.2			
21.5	42.6	58.9	4.2	1.1	1.2	
22.0	48.2	74.2	16.8	1.1		
22.5	29.1	79 6	31.4			2.2
23.0	23.5	58.9	69.2	4.6		
23.5	19.0	36.0	72.3	5.7		1.1
24.0	3.4	30.5	63.9	9.2		
24.5	4.5	12.0	54.5	5.7		
25.0	2.2	7.6	44.0	20.7	1.2	
25.5		6.5	18.9	14.9	10.1	
26.0		9.8	51.4	21.8	11.3	
26.5		1.1	23.1	12.6	7.5	
27.0	1.1	1.1	12.6	9.2	7.5	
27.5			11.5	8.0	1.2	
28.0			3.1	1.1		
28.5			4.2			
29.0			1.0		1.2	
29.5				1.1		
30.0			2.1	1.1	1.2	
30.5			1.0	2.3	1.2	
31.0				4.6	7.5	
31.5			1.0	1.1	3.8	1.1
32.0				6.9	3.8	2.2
32.5		1.1			1.2	1.1
33.0				2.3	6.3	1.1
33.5				1.1		1.1
34.0				1.1	1.2	3.3
34.5			1.0			2.2
35.0					1.2	4.5
36.0				1.1	2.5	4.5
36.5						4.5
37.0			2.1		2.5	4.5
37.5						2.2
38.0					1.2	3.3
38.5			1.0			2.2
39.0						1.1
39.5				1.1		3.3
40.0			1.0			5.6
40.5					2.5	1.1
41.0		1.1				2.2
42.0						1.1
42.5						1.1
44.5						1.1

LONG-TERM CADMIUM STRESS IN THE CUNNER, *TAUTOGOLABRUS ADSPERSUS*

J. R. MacInnes, F. P. Thurberg, R. A. Greig, and E. Gould[1]

ABSTRACT

The cunner, *Tautogolabrus adspersus,* was exposed for 30 and 60 days to 0.05 or 0.10 ppm Cd as cadmium chloride. The mean gill-tissue respiratory rates exhibited by the control fish and those exposed to 0.05 and 0.10 ppm Cd were 972, 736, and 665 μl O_2/h·g dry weight, respectively, after 30 days and 1,036, 702, and 587 μl O_2/h·g, respectively, after 60 days. Changes were also observed in the activities of two liver enzymes, aspartate aminotransferase (depression) and glucose-6-phosphate dehydrogenase (induction). Results are compared with those from other metal-exposure studies with cunners and other teleosts.

In recent years cadmium has become the subject of numerous investigations to determine its toxicity to various marine animals. These studies have progressed from short-term exposures to determine the concentrations that cause death (Eisler 1971; National Oceanic and Atmospheric Administration 1974; Westernhagen and Dethlefsen 1975), to long-term exposure studies to measure physiological change caused by very low levels (parts per billion, ppb) of cadmium (Eisler 1974; Calabrese et al. 1975; Dawson et al. in press; Gould in press; Thurberg et al. in press). Such long-term physiological stress can lower an animal's capacity to adapt to and survive in its natural environment.

In a recent collaborative study, a common coastal fish, the cunner, *Tautogolabrus adspersus,* was exposed to cadmium for 96 h and examined for changes in respiration, osmoregulation, cadmium uptake, histopathology, enzyme chemistry, and immune response (National Oceanic and Atmospheric Administration 1974). In the present study, cunners were exposed to cadmium for up to 60 days so that the effects of both exposure regimes might be compared. Parameters selected for study were gill-tissue oxygen consumption, liver enzyme activity, and cadmium uptake by various tissues.

Respiratory activity, a good indicator of the general condition of a fish, has been related to stress caused by such environmental variables as temperature (MacLeod and Pessah 1973), salinity (Olson and Harrel 1973), and heavy-metal pollutants (Calabrese et al. 1975). Gill-tissue respiration correlates well with whole-animal respiration, particularly the standard or inactive rate of oxygen consumption (Vernberg 1956; Thurberg et al. 1975). Thurberg and Dawson (1974) found that a 96-h exposure to 3 ppm Cd caused a depression in the cunner's rate of gill-tissue oxygen consumption. The present study examines the oxygen-consumption rates in excised gill tissue of cunners exposed to lower cadmium concentrations for much longer periods of time.

Because the fish were small, biochemical testing was restricted to the relatively large liver tissue mass. Two enzymes were selected for assay: a key enzyme of nitrogen metabolism that had been tested in the earlier, short-term exposure of cunners to high levels of cadmium (Gould and Karolus 1974), and a magnesium-linked enzyme whose activity in winter flounder, *Pseudopleuronectes americanus,* tissues is affected by the fish's exposure to sublethal levels of cadmium (Gould in press). The first enzyme, aspartate aminotransferase (E.C.3.6.1.1.; AAT), is linked to the production of animal energy (Gould et al. 1976), and in cunners exposed to 24 ppm Cd for 96 h, activity in the liver dropped to 40% of control activity (Gould and Karolus 1974). The second enzyme tested, glucose-6-phosphate dehydrogenase (E.C.1.1.1.49; G6PdH), is the first step in a glycolytic pathway that produces metabolites for reductive biosyntheses, and is found in abnormally high amounts in tissues having the high metabolic rates that often accompany stress (Weber 1963).

Besides the respiratory and enzyme studies,

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chemical analyses were performed to determine the cadmium uptake of certain tissues.

METHODS AND MATERIALS

Cunners for this study were trap-collected in Long Island Sound near Milford, Conn., during the summer of 1974 and held in the laboratory for 1 to 2 wk in flowing, sand-filtered seawater prior to cadmium exposure. They were fed Purina Trout Chow[2] throughout the holding and exposure periods. Beginning in August and ending in October 1974, the cunners were exposed in aerated, 285-liter fiber glass tanks filled to 228 liters with sand-filtered seawater (24±2‰ salinity, 22±2°C) by a proportional-dilution apparatus (Mount and Brungs 1967). This diluter controlled the intermittent delivery of toxicant-containing water to each tank throughout the exposure period at a flow rate of 1.5 liters every 2.5 min. This flow rate provided approximately four complete exchanges of water daily in each tank. Cadmium was added as $CdCl_2 \cdot 2\frac{1}{2}H_2O$ at concentrations of 0.05 and 0.10 ppm Cd. Background level of cadmium in the seawater was less than 0.001 ppm. Four tanks were used per concentration and control, with 15 fish in each tank, for a total of 60 fish per test level. The fish averaged 55.7 g in weight (range, 32.5-96.9 g) and 157 mm total length (range, 133-185 mm). After 30- and 60-day exposure periods, fish were removed for testing.

For oxygen-consumption measurements, two gills were dissected from each fish and placed in a 15-ml Warburg-type flask containing 5 ml water from the corresponding experimental tank. Oxygen consumption was monitored over a 4-h period at 20°C in a Gilson Differential Respirometer with a shaking speed of 80 cycles/min. Rates of oxygen uptake were calculated as microliters of oxygen consumed per hour per gram dry weight gill tissue ($\mu l\ O_2/h \cdot g$), including the gill arch, corrected to microliters of dry gas at standard temperature and pressure.

Liver tissue was taken for enzyme testing. Pools comprising liver samples from two fish were placed in small plastic pouches from which air was subsequently excluded, then sealed and stored frozen at −29°C. No more than 2 wk elapsed between the end of the exposure period and testing, as both AAT and G6PdH have been found to lose some activity after a month's frozen storage of whole liver tissue. For testing, each liver sample was homogenized 1:9, wt/vol, with iced, doubly glass-distilled water in a small, conical-tip glass homogenizer containing 25-μm glass powder to facilitate grinding. Centrifugation was at 17,000 g and 4°C for 45 min. The supernatant fractions were removed with Pasteur pipettes, diluted 1:1.5 with the iced water, vol/vol, and recentrifuged under the same conditions. The resulting supernates served as the 4% liver preparations. Protein determinations were made by the biuret method (Gornal et al. 1949), with modifications by Layne (1957), using a crystallized bovine serum albumin standard. The coupled spectrophotometric assay for AAT was the same as that used in the acute, short-term exposure of cunners to cadmium described by Gould and Karolus (1974). For G6PdH, both assay medium and spectrophotometric procedures have also been described elsewhere (Gould in press). Unit of activity was micromoles NADH oxidized (AAT) or NADP reduced (G6PdH) per minute per milligram protein.

Gill, muscle, and liver tissues were analyzed for cadmium uptake using the method described by Greig et al. (1975), in which the samples were wet-ashed with concentrated HNO_3, taken up in 10% HNO_3, and analyzed directly by atomic absorption spectrophotometry. Values were calculated on a wet-weight basis.

RESULTS AND DISCUSSION

Mortality and Respiration

Table 1 shows the actual and adjusted mortality data after 30- and 60-day exposures. Mortality data for the exposed fish were corrected for natural mortality of the controls by using Abbott's formula (Finney 1971), and can be interpreted as wholly attributable to cadmium stress. Clearly, exposure to low levels of cadmium increased the incidence of mortality, more so at 0.1 ppm than at 0.05 ppm.

TABLE 1.—Actual and adjusted percent mortality of cadmium-exposed cunner, *Tautogolabrus adspersus*.

Exposure concentration (ppm Cd)	Mortality (%)			
	30 days		60 days	
	Actual	Adjusted[1]	Actual	Adjusted[1]
0.00	3.3 (2)[2]	—	7.5 (5)	—
0.05	10.0 (6)	6.9	18.3 (10)	11.7
0.10	15.0 (9)	12.1	37.4 (20)	32.3

[1]Adjustments made by Abbott's formula (Finney 1971).
[2]Number dead out of 60 fish.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Gill-tissue oxygen consumption rates of cadmium-exposed cunner, *Tautogolabrus adspersus*.

Exposure concentration (ppm Cd)	Number of fish	Oxygen consumption rates[1] X	SE	Range	Level of significance[2]	
30 days:						
0.00	10	972	101	754-1,436		
0.05	10	736	46	530- 926	$P < 0.05$	$P < 0.025$
0.10	12	665	57	420- 967	NS	
60 days:						
0.00	5	1,036	94	788-1,324		
0.05	5	702	37	612- 831	$P < 0.01$	$P < 0.005$
0.10	5	587	62	472- 810	NS	

[1]Microliters O_2 per hour per gram dry weight.
[2]Student's *t*-test.

Gill-tissue oxygen consumption was significantly reduced after both 30- and 60-day exposures to 0.05 and 0.10 ppm Cd (Table 2), a result similar to that reported by Thurberg and Dawson (1974) in cunners exposed to 3 ppm Cd for 96 h. The depression was more pronounced at the end of the 60-day than at the end of the 30-day exposure. In another chronic exposure study, Dawson et al. (in press) found that gills of juvenile striped bass, *Morone saxatilis*, exposed to 0.5, 2.5, or 5.0 ppb Cd for 30 and 90 days, consumed significantly less oxygen than did the controls. The concentrations used were less than one-tenth of those used in the present study, but they still produced significant respiratory changes. The results reported here are also supported by a study using the winter flounder (Calabrese et al. 1975), in which fish exposed to 5 or 10 ppb Cd for 60 days showed significantly reduced oxygen consumption rates.

Exposure to silver also depresses cunner gill-tissue respiration (Thurberg and Collier in press). There is some evidence, however, that other metals affect fish respiration differently. Cunners exposed to 5 or 10 ppb mercury (as $HgCl_2$) for 30 and 60 days had significantly elevated respiration rates after 30 days, but normal respiration after 60 days (unpubl. data). Similarly opposite effects of the two metals, mercury and cadmium, were reported for the winter flounder in 60-day exposure studies (Calabrese et al. 1975); i.e., mercury elevated the oxygen consumption rate, whereas cadmium lowered it.

Enzyme Activity

In the liver of cunners exposed for 30 days to 0.1 ppm cadmium as chloride, AAT activity was significantly lower ($P<0.02$) than in control fish (Table 3). The drop in activity, about 20%, corroborates the effect of cadmium on liver AAT observed in cunners exposed for 4 days to high concentrations (24 ppm Cd) of this metal salt (Gould and Karolus 1974). As is the case with all aminotransferases, pyridoxal phosphate is an absolute requirement for activity. Because the biosynthesis of this essential cofactor requires a divalent metal cation (Meister 1955), and because cadmium affects enzymes requiring or reacting with divalent metal cations (Gould in press), it seems probable that cadmium's inhibitory effect on AAT activity is at the point of pyridoxal phosphate synthesis.

Liver G6PdH in cunners exposed for 30 days to 0.05 ppm Cd was significantly higher ($P<0.05$) than in controls (Table 3), and at 0.1 ppm the

TABLE 3.—Aspartate aminotransferase and glucose-6-phosphate dehydrogenase in the liver of cunner, *Tautogolabrus adspersus*, exposed for 30 days to cadmium chloride.

Exposure concentration (ppm Cd)	No. of sample pools	Enzyme activity[1] X	SE	Range	Level of significance[2]	
AAT:						
0.00	6	233	12	194-281		
0.05	6	217	14	160-254	$P < 0.02$	
0.10	6	181	13	154-234		
G6PdH:						
0.00	6	75	11	54- 91		
0.05	6	123	22	78-149	$P < 0.05$	$P < 0.001$
0.10	6	169	12	148-224	$P < 0.01$	

[1]Unit of activity = micromoles NADH oxidized (AAT) or NADP reduced (G6PdH) per minute per milligram protein.
[2]Student's *t*-test.

increase was very highly significant ($P<0.001$). This observation points to elevated pentose shunt activity in the livers of exposed fish. We construe this to be a compensatory mechanism, providing metabolites for increased rates of biosyntheses, to enable impaired biochemical systems to maintain near-normal function. Similar inductive response after sublethal metal challenge has been observed in other teleosts, such as the winter flounder: elevated levels of two metalloenzymes in the kidney and hematopoietic tissue after 60 days' exposure to 0.01 ppm Cd (Gould in press), and elevated levels of ornithine decarboxylase, another pyridoxal phosphate enzyme, in the liver and kidney after intravenous injection of methylmercury, following an initial drop in activity (Manen et al.[3]).

Chemical Uptake

Gill, muscle, and liver tissues from each exposure group were analyzed for cadmium uptake. In contrast to the marked cadmium uptake in tissues of cunners exposed for 96 h to cadmium at levels up to 48 ppm (Greig et al. 1974), nearly all the samples from these 30- and 60-day exposures to both 0.05 and 0.1 ppm Cd, as well as controls, were below the limits of detection (ca. 2 ppm, wet wt) for the sample size and procedure used.

CONCLUSIONS

In summary, long-term exposures of the cunner to 0.1 ppm Cd caused increased mortality, depressed gill-tissue oxygen consumption, and lowered transaminase and elevated pentose shunt activity in the liver.

The toxicity of cadmium to marine animals is influenced, however, by such environmental variables as temperature, salinity, pH, dissolved oxygen (Gardner and Yevich 1969; Vernberg and Vernberg 1972), and chemical form (Gould et al. 1976). Moreover, toxicity of cadmium varies with different species: Westernhagen et al. (1974) and Westernhagen et al. (1975) found that low salinities enhance the toxicity of cadmium to the developing eggs of herring, *Clupea harengus,* and needlefish, *Belone belone,* but Westernhagen and Dethlefsen (1975) reported no such enhancement using flounder, *Pleuronectes flesus,* eggs, possibly because of the differences in the capacity of the egg membranes to bind cadmium ions. The nature and degree of cadmium's toxicity may well change under different laboratory or field conditions.

[3]Manen, C. A., B. Schmidt-Nielsen, and D. H. Russell. 1976. Alterations of polyamine synthesis in liver and kidney of winter flounder in response to methylmercury. Unpubl. manuscr. Univ. Ariz. Med. Cent., Dep. Pharmacol., Tucson, and The Mt. Desert Island Mar. Biol. Lab., Salsbury Cove, Maine.

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MATURATION AND INDUCED SPAWNING OF CAPTIVE PACIFIC MACKEREL, *SCOMBER JAPONICUS*

RODERICK LEONG[1]

ABSTRACT

Pacific mackerel, *Scomber japonicus*, became sexually mature under laboratory conditions and were induced to spawn with hormone injections. Fish caught before the major spawning season became mature under the natural photoperiod and under artificial photoperiods of 4 h light 20 h dark, 8 h light 16 h dark, and 16 h light 8 h dark. Mackerel caught near the end of the spawning season redeveloped their gonads more rapidly at 18°C than at 15°C or ambient temperature. A 16°C-14 h light 10 h dark environment was effective in maintaining mackerel in spawning condition beyond the normal spawning season. Any of three combinations of hormones induced spawning: gonadotropin from ground salmon pituitary followed 24 h later by gonadotropin from pregnant mare serum; human chorionic gonadotropin followed 24 h later by gonadotropin from pregnant mare serum; and salmon pituitary plus human chorionic gonadotropin followed 24 h later by salmon pituitary plus human chorionic gonadotropin plus gonadotropin from pregnant mare serum. The hormones did not induce spawning when used individually. A procedure for routine spawning of Pacific mackerel is described.

Laboratory studies of the biology of pelagic fish larvae are often limited by the uncertainty of collecting eggs at sea. An alternative to collecting eggs at sea is the maturation and spawning of fish in the laboratory. This objective was met for the northern anchovy, *Engraulis mordax* (Leong 1971). Another species whose larvae are under study at the Southwest Fisheries Center is the Pacific mackerel, *Scomber japonicus* Houttuyn, but the eggs are not available off the southern California coast during most of the year. To increase the availability of mackerel eggs for experimental work, I began a study designed to develop procedures for routinely spawning mackerel on demand throughout the year. My approach was to first find a suitable photoperiod-temperature environment which would encourage maturation and to subsequently induce spawning with gonadotropic agents. This report contains observations on the maturation of mackerel under different photoperiod-temperature conditions in the laboratory; results of exploratory tests with hormones to induce spawning; and a description of a procedure currently used to spawn mackerel.

I followed the maturation of mackerel under four photoperiods (4 h light 20 h dark, 8L16D, 16L8D, and ambient day length) and three temperatures (15°C, 18°C, and ambient 12.8° to 19°C). I also examined the effectiveness of a 16°C-14L10D environment for maintaining mackerel in spawning condition after the normal spawning season. The hormones tested for the induction of spawning were gonadotropin from ground salmon pituitary, human chorionic gonadotropin, and gonadotropin from pregnant mare serum. The importance of the photoperiod-temperature environment in regulating maturation in fish and the use of gonadotropins for inducing spawning are well known from the early review of Pickford and Atz (1957), but observations on marine pelagic species are still limited. These are the first observations on the maturation and spawning of a scombrid fish under laboratory conditions.

METHODS

Maturation of Mackerel Under Four Photoperiods

Knaggs and Parrish (1973) examined the ovaries of mackerel from the commercial catch and concluded that *S. japonicus* can spawn from March through October but that the majority spawn from April through August. Kramer (1960), using sea-caught larvae as criteria, concluded that spawning occurs from late April or early May to August.

The fish used in these experiments were caught off the southern California coast by hook and line

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between 1 February and 7 March 1973. The dates of capture were 1 to 2 mo in advance of the major spawning season. The fish ranged from 325 to 340 mm fork length; most fish of this size are capable of spawning (Knaggs and Parrish 1973). During the period of collection, the fish were held under continuous incandescent lighting and a temperature of 19°C. These were arbitrary holding conditions.

On 14 March, 1 wk after the last fish was captured, the mackerel were divided into four groups and placed in three indoor plastic swimming pools (4.6 m in diameter, 1 m water depth) and one outdoor pool (7.3 m in diameter, 1 m water depth). Each of the three indoor pools was enclosed in a separate room lined with black opaque polyethylene film. A 200-W incandescent bulb, 1.2 m above the water surface, illuminated each indoor pool during the artificial day. A timer-controlled rheostat gradually lit and dimmed the bulb over 30 min to avoid startling the fish. The length of day was considered as the time of full illumination. Two 3-W lamps, 1 m above the water surface, burned continuously and provided low-level illumination during the dark period. The light intensity was about 215 lx at the brightest spot on the surface during the day and less than 5.4 lx at night. The outdoor pool was shielded from direct sunlight by an opaque plastic canopy 1.2 m above the water surface but the sides were open and the fish received a natural photoperiod.

Temperature control was achieved with a commercial temperature regulator and mixing valve unit which automatically adjusted the inflow of chilled (10°C) and heated (20°C) seawater to maintain a desired pool temperature. For this series of observations the temperature was set at 19° ± 0.5°C for all tanks. I chose this temperature because captive mackerel had spawned at this temperature during a preliminary study. The flow rates were 32 liters/min for the indoor tanks and 50 liters/min for the outdoor tank. Each tank also had a recirculating pump of 250 liters/min capacity.

Each of the experimental groups contained 50 fish. Commencing on 17 March, the three groups of fish in the indoor tanks were maintained on photoperiods of 4L20D, 8L16D, and 16L8D, respectively. The group of fish in the outdoor tank remained under the natural photoperiod where the time between sunrise and sunset was 12 h. Biopsy samples of the gonads were taken prior to the photoperiodic change and again a month later to note the change in maturation. The biopsies were taken by inserting the tip of a glass pipette (1.2 mm in diameter) through the genital pore of a fish anesthetized in 7 ppm quinaldine and removing a small piece of gonad by mild suction. The technique, a modification of that used by Stevens (1966), did not appear to cause permanent damage to the fish. All ovarian samples were examined with a dissecting microscope and the diameter of the largest eggs measured to the nearest 0.1 mm. No effort was made to categorize the males except to note if milt was obtained. Six females were biopsied at the start of the trial and two from each treatment at the end.

An egg strainer was positioned at the outflow of each tank and inspected daily to detect spontaneous spawning. The strainer, a 1 × 1 × 0.2 m wooden frame with 202-μm mesh netting stretched across the bottom, was partially immersed in a water bath to prevent desiccation of eggs. The mackerel were fed daily with either freshly thawed frozen anchovies or ground squid. Occasionally, Oregon moist chow was mixed in with the ground squid as a supplement. The estimated daily ration was 4% of body weight.

Maturation of Mackerel Under Ambient, 15°C, and 18°C Temperatures

Mackerel judged to be in or near postspawning condition were collected between 23 August and 28 September 1973. The fish ranged from 330 to 370 mm fork length and were kept indoors at 18°C-14L10D during the period of collection. The mackerel were subsequently divided into three groups of 50 fish each and placed in two of the indoor pools and in the outdoor pool already described. Beginning on 3 October, the two groups of indoor fish were kept at 15°C and 18°C, respectively. The fish in the outdoor tank received seawater at ambient temperature (19°C at the outset) which fluctuated with ocean conditions at the intake. The intake was located at the end of the pier at the Scripps Institution of Oceanography, La Jolla. The photoperiods were 14L10D for both indoor groups and natural for the outdoor group. Six females were biopsied at the start of the trial for ova measurements. Several fish from each group were biopsied at various intervals afterwards until March 1974 to observe changes in ovarian development. I attempted to obtain eggs from at least two females per group with every round of sampling.

Test of a 16°C-14L10D Environment for Maintaining Mackerel in Spawning Condition After the Normal Spawning Season

The group of 50 fish that was held outdoors under ambient conditions began to spawn spontaneously at the end of April 1974. On 7 July, while some spawning was still in progress, 25 fish were transferred indoors to a tank with ambient temperature (19°C) seawater and photoperiod of 14L10D. On 8 July, the temperature was lowered to 16°C and the fish were kept at that temperature for 9 mo. Biopsies were taken at the time of transfer and in each succeeding month to determine if at least one female was in spawning condition. During each sampling, fish were catheterized until a female with 0.7-mm diameter eggs was found. Females with eggs of this size are functionally mature, i.e., can be spawned with hormone injections.

Testing of Hormones for Induction of Spawning

The agents tested for the induction of spawning were gonadotropin from ground chinook salmon, *Oncorhynchus tshawytscha,* pituitary (SP), human chorionic gonadotropin (HCG), and gonadotropin from pregnant mare serum (PMS). The agents were applied individually and in combination, as indicated in Table 1.

The salmon pituitaries were collected, preserved, and prepared as described by Haydock (1971). The carrier for all injections was saline and the injection volume 0.1 ml. The injections were applied intramuscularly near the base of the dorsal fin with a 24-gauge needle on a 0.5-ml syringe.

The mean weight of the fish was 0.9 kg (range 0.8 to 1.1 kg). Dosages were not adjusted for differences in fish weight, and one male and one female were injected for each treatment. The fish had become sexually mature in the laboratory and were among those used in the photoperiodic experiment. The injection trials were carried out during June through August which is also the time of spawning in nature.

Fish were biopsied beforehand and only males with generous amounts of milt and females with 0.7-mm diameter eggs were injected (preliminary testing indicated that the eggs had to be close to 0.7 mm in diameter before the hormones would stimulate a noticeable response). The injected pair was isolated in a small swimming pool (3 m in diameter, 0.5 m water depth) with water temperature at 17°C and a flow rate of 2.5 liters/min. An egg strainer was placed at the outflow to detect spawning. Biopsies and general observation were

TABLE 1.—Results of tests with gonadotropin from ground salmon pituitary (SP), human chorionic gonadotropin (HCG), and gonadotropin from pregnant mare serum (PMS) for induction of spawning in *Scomber japonicus*.

Hormones and dosages				After 24 h[2]					After 40 h					Results of stripping[4]	
First injection		Second injection[1]		Egg diameter[3] (mm)	Not ovulated	Ovulated	Spawned	Female dead	Female alive	Egg diameter (mm)	Not ovulated	Ovulated	Spawned	Female dead	Female alive	Number eggs	Number live larvae
Hormone	Dosage	Hormone	Dosage														
SP	1 mg	—	—	0.8	X				X	1.1		X			X	<500	<10
SP	5 mg	—	—	0.8	X				X	1.1		X		X		—	—
SP	10 mg	—	—	1.1		X		X						—		—	—
SP	15 mg	—	—	1.1		X			X					X		<500	<10
SP	25 mg	—	—	0.9	X				X	1.1		X		X		—	—
HCG	12.5 IU	—	—	0.8	X				X	1.1		X			X	<500	<10
HCG	25 IU	—	—	0.8	X				X	1.1		X			X	<500	<10
HCG	50 IU	—	—	0.9	X				X	1.1		X		X		—	—
HCG	125 IU	—	—	1.1		X		X						—		—	—
HCG	250 IU	—	—	1.1		X			X					X		<500	<10
HCG	500 IU	—	—	1.1		X			X					X		<500	<10
PMS	300 IU	—	—	0.8	X				X	0.8	X				X	—	—
PMS	750 IU	—	—	1.1		X			X	·					X	<500	<10
PMS	1,000 IU	—	—	0.8	X				X	1.1		X			X	5,000	<10
SP	1 mg	PMS	100 IU	0.9	X				X	1.1			X		X	50,000	10,000
HCG	12.5 IU	PMS	100 IU	0.8	X				X	1.1			X		X	30,000	10,000
SP	1 mg	SP	1 mg	0.9	X				X	1.1			X		X	80,000	30,000
+		+															
HCG	12.5 IU	HCG	12.5 IU														
		+															
		PMS	200 IU														

[1]Second injection given 24 h after first injection.
[2]Time measured after first injection.
[3]Egg diameter was 0.7 mm before first injection.
[4]Stripping was attempted on live fish with ovulated eggs. Stripping was attempted even if a fish spawned because the eggs were unfertilized.

taken at 24 and 40 h after injection to note the effects of the hormones. If ovulation or spawning had occurred, stripping was attempted and the eggs fertilized by the dry method (Davis 1961).

RESULTS

Maturation of Mackerel Under Four Photoperiods

The female mackerel caught before the spawning season became mature in the laboratory under the three constant photoperiods (4L20D, 8L16D, and 16L8D) and under ambient light conditions. At the start of the experiment (17 March) the diameter of the largest eggs sampled from the six females ranged from 0.4 to 0.6 mm. Thus, the females were not fully mature but two of the males sampled already had milt and may have been capable of spawning. Recently spawned eggs appeared in the egg strainer of the 16L8D tank on 17 April, 1 mo after the beginning of the experiment. Catheterization of two females from each treatment showed that all treatments contained females with 0.7-mm diameter eggs indicating sexual maturity. None of the treatments appeared to inhibit maturation. The results indicated that female mackerel in prespawning condition will become sexually mature in the laboratory under a wide range of photoperiods at 19°C.

The dates of initial spawning showed no relation to the length of day. Spawning was detected in the 4L20D tank on 25 April and in the outdoor tank on 1 May 1973. In the outdoor tank, the time between sunrise and sunset had lengthened from 12 h at the start of the trial to 13½ h on 1 May. Spawning was never detected in the 8L16D tank although it contained functionally mature males and females.

The mackerel spawned during the dark period but the exact time is not known. Watanabe (1970) stated that mackerel spawn between 2000 and 2400 h in nature. Spawning occurred three or four times a week in the outdoor pool and two or three times a week in the indoor pools from May to mid-June. The frequency of spawning then decreased and was rare by mid-July when observations ended.

Although the fish spawned spontaneously, the predictability of spawning and the viability of eggs were not satisfactory. The number of eggs collected per day was usually less than 3,000, although one collection was over 50,000. The percentage of viable eggs seldom exceeded 10% and was often zero. The spontaneously spawned eggs were translucent and of the proper size, 1.1 mm in diameter, but most were not fertilized.

Observations ended in mid-July because the fish began to feed poorly and started to die. An accompanying symptom of failing health was the malformation of jaws in about half of the fish. Afflicted fish swam with their jaws constantly agape and were unable to bite on food items. The condition may have been partly due to the high water temperature as some fish recovered when transferred to a tank with 15°C seawater. Thus, while the mackerel became fully mature at 19°C a prolonged exposure may be detrimental.

Maturation of Mackerel at Ambient, 15°C, and 18°C Temperatures

Mackerel captured near the end of the spawning season redeveloped their ovaries more rapidly at 18°C than at 15°C or ambient temperature (Figure 1). Three of the females sampled at the start of the trial, 3 October, had eggs 0.7 mm in diameter while three others had eggs 0.2 mm in diameter. This difference in egg size can be expected near the end of the spawning season as some females stop spawning and begin resorption of ovaries earlier than others. In November, one female from the 18°C treatment still had eggs 0.7 mm in diameter but four other fish from that treatment and five from each of the other two treatments could not be sexed because of immaturity of the gonads. Below a certain stage of maturity gonads are too small to remove tissue for biopsy. Biopsies were still difficult to perform in January and samples were obtained from less than half of the fish. The females that did provide samples had eggs measuring 0.3 to 0.4 mm in diameter. Biopsies were more successful in February; the females from the 15°C and ambient temperature groups still had eggs measuring 0.3 to 0.4 mm in diameter but two females from the 18°C group had eggs of 0.5 and 0.6 mm in diameter, respectively. Two of the three females sampled from the 18°C group on 20 March had eggs of 0.7 mm in diameter and one was spawned with hormone injections. The spawning date was about 5½ mo after the start of the trial. On 20 March, the females from the 15°C and ambient temperature groups did not as yet have eggs exceeding 0.5 mm in diameter. Observations ended shortly after for the 15° and 18°C

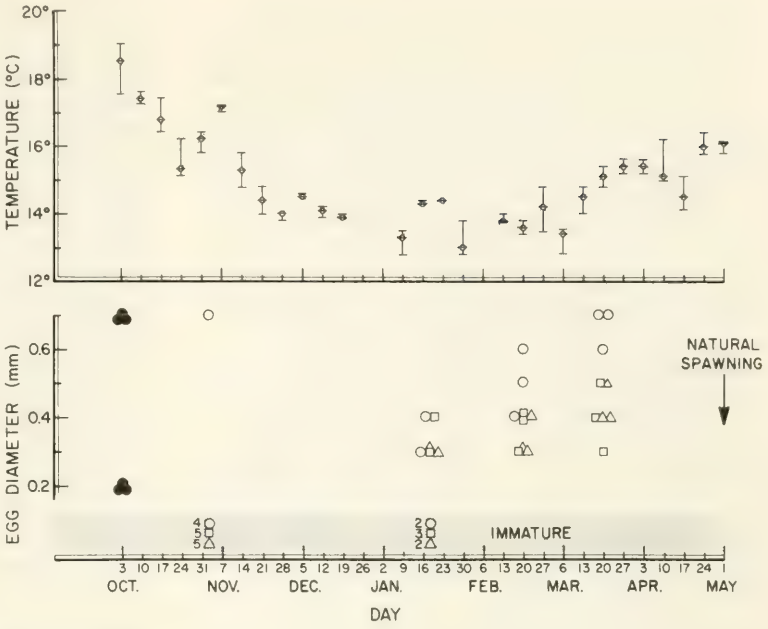

FIGURE 1.—Development of eggs in female *Scomber japonicus* under three temperature conditions. Upper panel, weekly ambient temperature ranges and medians. Lower panel, diameter of the largest eggs in individual females under 18°C, 15°C, and ambient temperatures. Shaded area, numbers of individuals which could not be sexed due to immaturity. Closed circles represent egg diameters in initial sample, open circles at 18°C, squares at 15°C, and triangles at ambient temperature. Arrow indicates when group under ambient conditions spawned naturally.

groups because of a water system failure and total loss of fish indoors.

The fish in the outdoor tank survived and began to spawn spontaneously on 30 April, nearly 6 wk after the induced spawning. The end of April is also the approximate time that the natural population begins to spawn off the southern California coast (Kramer 1960). The temperatures in the outdoor tank were very similar to the temperatures at Scripps Pier, which can be considered indicative of surface coastal conditions off southern California (Radovich 1961). Thus the mackerel in the outdoor tank should have received temperatures which were like the temperatures found in the southern California spawning grounds and the similar time of initial spawning may be expected. However, it should be pointed out that mackerel in the wild can migrate over long distances (Roedel 1952) and the average temperature cycle they undergo in nature is not precisely known.

The temperature in the outdoor pool at the time of initial spawning was 16°C which is a favorable temperature for mackerel spawning in nature. Kramer (1960), utilizing data from the California Cooperative Oceanic Fisheries Investigations surveys, found mackerel larvae occurring at temperatures (taken at 10 m) ranging from 10.3°C to 26.8°C with more than 68% of all occurrences between 14.0° and 17.9°C. Watanabe (1970), using Japanese data, found early stage mackerel eggs occurring between temperatures (taken at the surface) of 13° and 23°C with the mode of positive stations between 16° and 19°C.

Test of a 16°C-14L10D Environment for Maintaining Mackerel in Spawning Condition After the Normal Spawning Season

The group of 25 fish that was placed under a 16°C-14L10D environment contained functionally mature individuals at the start of the trial, 7 July. Monthly biopsies indicated that at least one female in the group was sexually mature from July 1974 through March 1975. The months of sampling included December, January, and February when the maturity indices of mackerel are at the lowest levels (Knaggs and Parrish 1973). No more than three females were catheterized in any month before one with 0.7-mm diameter eggs was found. The eggs in the other females ranged from 0.2 to 0.6 mm in diameter. I am not certain if the ripe females remained sexually mature continuously or if they resorbed and subsequently redeveloped their ovaries.

Effectiveness of Hormones for the Induction of Spawning

All injections of ground salmon pituitary (SP) from 1 to 25 mg stimulated hydration and ovula-

tion but the females did not spawn spontaneously nor could they be satisfactorily stripped (Table 1). The females ovulated within 24 h in the 10- and 15-mg trials and between 24 and 40 h in the 1-, 5-, and 25-mg trials. Ovulated eggs were catheterized from live fish in the 1- and 15-mg trials and from dead fish in the 5-, 10-, and 25-mg trials. The live females in the 1- and 15-mg trials were stripped as soon as ovulation was detected but the fish released only small numbers of eggs even with heavy stripping pressure. Attempted fertilization resulted in less than 10 larvae in both trials. The stripped eggs were translucent, measured 1.1 mm in diameter, and appeared normal but nearly all were not viable.

The females that received 5, 10, 15, and 25 mg of SP died within 40 h after injection. The female that received 1 mg was intentionally killed at 72 h for dissection. All of the females including the one that received only 1 mg of SP had severely distended abdomens. Subsequent dissection revealed that the distension was due to extremely enlarged ovaries. The ovaries contained many ovulated eggs which were not extruded and the females were apparently egg bound. I did not see any plugs or clots which impeded the flow of eggs.

All injections of SP, 1 to 25 mg, to male mackerel facilitated the stripping of milt. The milt in the catheter samples before injection was thick and only small amounts could be expressed. The injections of SP brought about a thinning of the milt and made stripping easier. None of the males injected with SP died.

All injections of human chorionic gonadotropin (HCG), 12.5 to 500 IU, stimulated hydration and ovulation but the females could not be easily stripped of eggs. Ovulation occurred within 24 h in the 125-, 250-, and 500-IU trials and between 24 and 40 h in the 12.5-, 25-, and 50-IU trials. None of the females that were alive when ovulation was detected could be stripped of more than 500 eggs. The number of larvae produced was negligible in all trials. All of the females that received 50 or more IU of HCG died within 40 h after injection. The females that received 12.5 or 25 IU of HCG were purposely killed at 72 h. As with SP, all of the females had severely distended abdomens and enlarged ovaries. All dosages of HCG facilitated the stripping of milt without killing the male.

The results of trials with pregnant mare serum (PMS) were variable. In the 1,000-IU trial the eggs increased in size from 0.7 to 0.8 mm in diameter in 24 h and were ovulated by 40 h. More than 5,000 eggs were stripped at 40 h but most of the eggs were cloudy, had collapsed perivitelline membranes, and were apparently overripe. However, a few eggs were viable and a small number hatched following fertilization. In the 750-IU trial, ovulation was detected at 24 h but the eggs already had collapsed perivitelline membranes and were overripe. The eggs in the 300-IU trial grew to 0.8 mm within 24 h but did not show further improvement at 40 h. None of the females injected with PMS had severely distended abdomens and none were dead by 40 h after injection. At all levels tested, PMS made the stripping of milt easier and did not kill the injected male.

The three combinations of hormones tested were all successful in stimulating hydration, ovulation, and spontaneous release of eggs. The first injection, 1 mg SP, of the SP-PMS trial promoted egg growth from 0.7 to 0.9 mm in diameter in 24 h. The second injection of 100 IU PMS 24 h later appeared to stimulate the release of eggs as 50,000 eggs were found in the egg strainer at 40 h. The eggs were translucent, measured 1.1 mm in diameter, and appeared to be of good quality but were unfertilized. However, the female extruded another 50,000 eggs when stripped at 40 h and these were artificially fertilized with milt from the injected male. About half of the eggs showed signs of cleavage and approximately 10,000 larvae hatched. The larvae appeared normal when compared with the larval descriptions of Kramer (1960) and Watanabe (1970). Some of the larvae later developed into juveniles which grew to more than 100 mm total length.

The other two combinations (12.5 IU HCG initially and 100 IU PMS 24 h later; 1 mg SP + 12.5 IU HCG initially and 1 mg SP + 12.5 IU HCG + 200 IU PMS 24 h later) produced similar results. The initial injection produced egg growth to 0.8 or 0.9 mm and spawning occurred after the second injection but the spawned eggs were unfertilized. The fish were then stripped and the eggs artificially fertilized. Many of these hatched and produced thousands of viable larvae. All of the females became bruised from the handling during stripping, and died a few days after spawning.

RECOMMENDED PROCEDURE

A procedure for spawning mackerel has been developed from the foregoing observations and the method has been used since March 1975 to routinely produce viable eggs. The 16°C-14L10D

environment is used to ripen and maintain spawnable stocks of fish in the laboratory and hormone injections are used to induce spawning. I use 1 mg SP + 12.5 IU HCG for the first injection followed by 1 mg SP + 12.5 IU HCG + 200 IU PMS 24 h later to spawn females and a 5-mg SP injection for spawning males. I inject two males to insure an adequate supply of milt. The procedure is essentially the same as described in the Methods section. The egg strainer is checked regularly beginning at 12 h after the second injection to the female and the female is examined whenever eggs are detected. The female is stripped if she releases eggs easily and the eggs are extruded into a dry finger bowl for fertilization. The male is stripped and the milt collected with a spoon held below the genital pore. The milt is washed into the finger bowl with a little seawater and the contents swirled gently for 3 min. The eggs are then placed in an incubation tank for further development and hatching. To date, induction of spawning has been successful 26 times in 36 attempts, each spawning producing 6,000 or more viable eggs, and successful spawning has been induced during every month of the year.

ACKNOWLEDGMENT

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NOTES

INCORPORATING SOAK TIME INTO MEASUREMENT OF FISHING EFFORT IN TRAP FISHERIES

While it is recognized that soak time (number of days a trap is allowed to fish before it is retrieved) is an important fishing strategy decision for the individual fisherman, there is surprisingly scarce information on the subject. Little data is available on the relationship between catch and soak time. Similarly, the implications of variable soak times have not been widely discussed.

This paper develops a model to determine the profit-maximizing soak time for an individual fisherman in the Florida spiny lobster, *Panulirus argus,* fishery. This establishes the relative importance of soak time as one of the components of fishing effort in trap fisheries and leads to suggestions for incorporating soak time into the traditional measurement of trap days to more accurately reflect fishing effort in trap fisheries.

Profit-Maximizing Soak Time

Catch per trap day was regressed on soak time with the data collected by Robinson and Dimitriou (1963). The best statistical fit using ordinary least squares is in the form of Equation (1) (Figure 1).

$$\frac{C}{D} = \frac{\alpha}{S^{\beta}} \tag{1}$$

where C = catch per trap haul
D = days fished for the sample
S = soak time in days
$\alpha = 2.94, \quad \hat{t}_{\alpha} = 5.40$
$\beta = 0.90, \quad \hat{t}_{\beta} = 11.25$
year: 1963
$n = 25$
$R^2 = 0.86.$

Since the number of days fished (D) in this field experiment was synonymous with the soak time ($D = S$), then:

$$C = \alpha S^{(1-\beta)}. \tag{2}$$

Taking the first and second derivatives of Equation (2) with respect to the soak time:

$$\frac{dC}{dS} = \frac{(1-\beta)\,\alpha}{S^{\beta}} > 0 \tag{3}$$

$$\frac{d^2C}{dS^2} = \frac{(\beta^2-\beta)\,\alpha}{S^{(1+\beta)}} < 0. \tag{4}$$

Equations (3) and (4) imply the catch per trap haul increases at a decreasing rate with respect to the soak time (Figure 2). This relationship seems

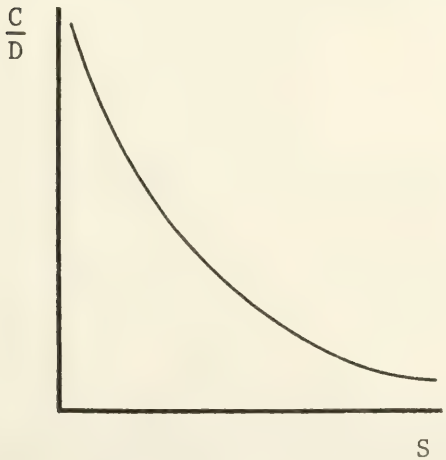

FIGURE 1.—Catch per day with respect to the soak time.

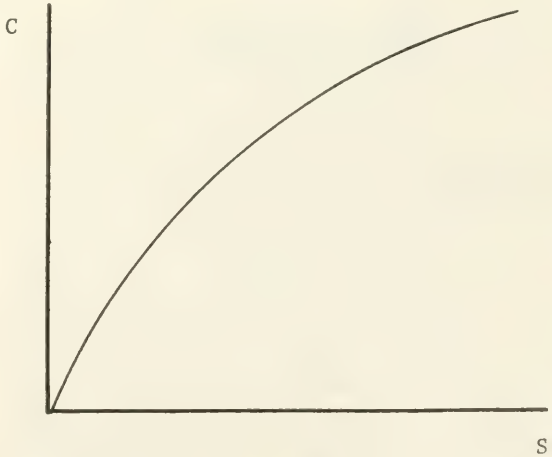

FIGURE 2.—Catch per haul with respect to the soak time.

reasonable for traps that attract fish because they are baited, or because the trap acts as a refuge, or some combination of both reasons. This relationship has been observed by Thomas (1973) in the Maine (American lobster, *Homarus americanus*) fishery and by Warner (pers. commun.) and Simmons (pers. commun.) for Florida Keys and Bahama spiny lobster trap fishing. The distinction would be that the catch curve for traps that are highly dependent on baiting would presumably be relatively steeper than for less bait-dependent traps reflecting the relative attracting power of the bait during the initial soak time.

In both cases it is expected that the total catch per trap haul would peak and perhaps even decrease with very long soak times either because of mortality in the trap (starvation, cannibalism, predation) or escapement. Therefore, while it is recognized that the catch per trap haul with respect to the soak time is probably sigmoidal shaped, the negatively sloped portion that would be associated with long soak times is excluded from the model on the assumption it is not within the range of normal commercial fishing strategies.

The number of times each trap is hauled in a given time period (e.g., 1 mo) is the number of days in the time period divided by the soak time (in days). The total catch for the given fishing period would be the catch per trap haul Equation (2) times the number of times each trap is hauled (D/S) times the number of traps (T).

$$L = \left[\alpha S^{(1-\beta)}\right]\left(\frac{D}{S}\right)(T) = \frac{\alpha DT}{S^{\beta}} \qquad (5)$$

where L = total catch in the fishing period
T = number of traps fished
D = number of days in the fishing period
S = soak time in days.

Taking the first and second derivatives of Equation (5) with respect to the soak time:

$$\frac{\partial L}{\partial S} = \frac{-\beta\alpha DT}{S^{(1+\beta)}} < 0 \qquad (6)$$

$$\frac{\partial^2 L}{\partial S^2} = \frac{(\beta + \beta^2)\,\alpha DT}{S^{(2+\beta)}} > 0. \qquad (7)$$

Equations (6) and (7) imply that, holding the number of traps constant, the total catch for the fishing period decreases at a decreasing rate with respect to the soak time (Figure 3). This is because a longer soak time increases the catch per trap haul but decreases the number of hauls possible in the fishing period.

FIGURE 3.—Total catch in the fishing period with respect to the soak time.

Holding the number of traps constant is a highly restrictive condition. The advantage of increasing the soak time would be to permit the individual fisherman to operate more traps. The most reasonable constraint measurement for fishing capabilities is a maximum number of hauls in a fishing period.

It is assumed an individual vessel can make a constant (maximum) number of hauls during the fishing period. This maximum is predicated on characteristics of the vessel, number in the crew, distance traps are set from port, depth of water, and weather conditions.

$$H \equiv \left(\frac{D}{S}\right)T \qquad (8)$$

$$H = K \qquad (9)$$

where H = total number of trap hauls in D days
K = maximum number of trap hauls in D days.

Substituting Equation (9) into Equation (8) and rearranging:

$$T = \frac{SK}{D} \qquad (10)$$

Substituting Equation (10) into Equation (5) results in a total catch equation where both the soak time and number of traps vary in combi-

nations that always result in the maximum number of possible hauls.

$$L = \left(\frac{\alpha D}{S^{\beta}}\right)\left(\frac{SK}{D}\right) = \alpha K S^{(1-\beta)}. \tag{11}$$

Taking the first and second derivatives of Equation (11) with respect to the soak time:

$$\frac{dL}{dS} = \frac{(1-\beta)\,\alpha K}{S^{\beta}} > 0 \tag{12}$$

$$\frac{d^2L}{dS^2} = \frac{(\beta^2-\beta)\,\alpha K}{S^{(1+\beta)}} < 0. \tag{13}$$

Equations (12) and (13) imply that, holding the number of total hauls constant, the total catch increases at a decreasing rate with respect to the soak time (Figure 4). This is because a longer soak time decreases the catch per trap day but increases the number of traps that can be fished.

The fisherman/entrepreneur is not interested in maximizing the catch per trap day, the catch per trap haul, or the total catch. He presumably wants to maximize the net economic return (profit) from fishing which is the difference between the total revenue and total cost of his fishing activities. The total revenue is equal to the ex-vessel price times the catch. In the case of an individual fisherman, it can normally be assumed that the price is constant over all catch ranges. This is because the catch of an individual fisherman is relatively small compared with total landings in the fishery and will, therefore, not have a significant influence on the prevailing ex-vessel prices.

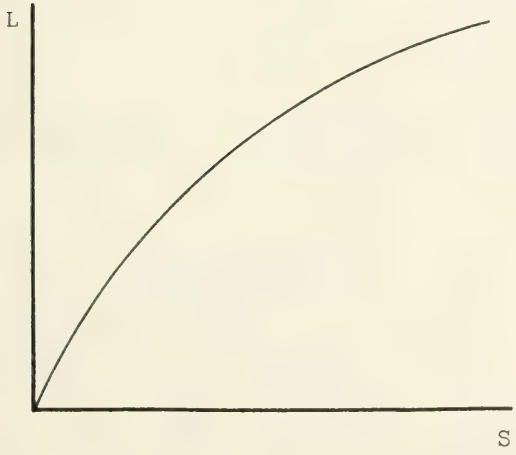

FIGURE 4.—Total catch in the fishing period with respect to the soak time, given combinations of soak time and number of traps that always result in the maximum number of hauls.

$$TR = \rho L \tag{14}$$

where TR = total revenue
ρ = ex-vessel fish price (per pound round weight).

Total fishing costs are comprised of fixed investment costs, trap hauling costs, and trap costs:

$$TC = I_K + H_K + \delta T \tag{15}$$

where TC = total fishing costs
I_K = fixed costs (e.g., vessel depreciation, insurance, routine maintenance) on equipment capable of K hauls in D days
H_K = costs of K hauls
δT = costs of traps
δ = unit cost (depreciated value and maintenance cost) of a trap for the fishing period (D days).

Trap hauling costs are treated as a constant in the model because the number of hauls is held constant. It is recognized that trap hauling costs are dependent on factors such as fishing depth and the distance traps are set from port as well as the number of trap hauls. This model assumes these factors are relatively constant. In the case of Florida spiny lobster fishing, this may not be too unreasonable an assumption because fishermen customarily fish the same area for considerable periods of time. When the assumption does not hold, neither does the assumption about a constant maximum number of hauls.

Since the model is an analysis of changes in soak time and traps fished, the constant costs in the model (I_K and H_K) play minor roles. It is assumed that with the profit-maximizing soak time and number of traps that total revenue will be greater than total costs. If total costs were greater than total revenue for all soak times and number of traps fished, then presumably fishermen would stop fishing to avoid incurring continuous losses. Profit (π) is defined as total revenue (Equation (14)) minus total costs (Equation (15)):

$$\pi = \rho L - I_K - H_K - \delta T. \tag{16}$$

Substituting Equations (10) and (11) into Equation (16):

$$\pi = \rho\left[\alpha K S^{(1-\beta)}\right] - I_K - H_K - \delta\left(\frac{SK}{D}\right). \quad (17)$$

Taking the first and second derivatives of Equation (17) with respect to the soak time:

$$\frac{d\pi}{dS} = \frac{(1-\beta)\,\rho\alpha K}{S^{\beta}} - \frac{\delta K}{D} \gtrless 0 \quad (18)$$

$$\frac{d^2\pi}{dS^2} = \frac{(\beta^2-\beta)\,\rho\alpha K}{S^{(1+\beta)}} < 0. \quad (19)$$

The profit-maximizing soak time can be determined by setting Equation (18) equal to zero and solving for S (Figure 5):

$$S_\pi = \left[\frac{(1-\beta)\,\rho\alpha D}{\delta}\right]^{\frac{1}{\beta}}. \quad (20)$$

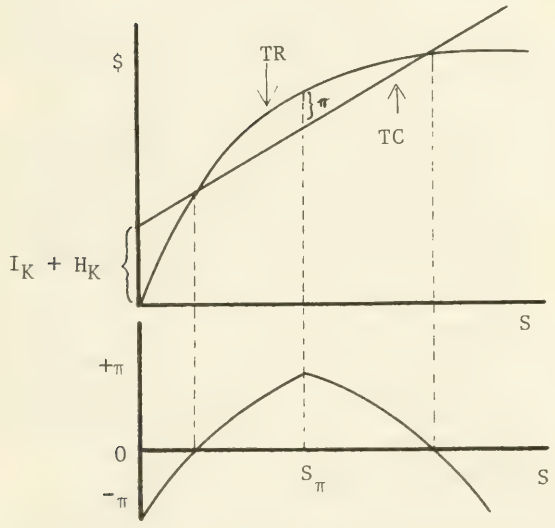

FIGURE 5.—Total revenue, total cost, and profit with respect to the soak time, given combinations of soak time and number of traps that always result in the maximum number of hauls.

The parameters prevailing in 1962 were:

Purchase price of a trap: \$6.00
Maintenance cost of a trap over its life span: (0.25)(cost) = \$1.50
Total cost of a trap: \$7.50
Estimated life span of a trap: 1.5 seasons or 12 mo
δ = depreciated value of a trap for D days use (1 mo)
δ = 63¢
ρ = 38.3¢
D = 30
α = 2.94
β = 0.90
S_π = 6.52 (as estimated by Equation (20)).

The theoretically profit-maximizing soak time compares favorably with the average soak time of 6-7 days in 1962 (October-December) observed by Robinson and Dimitriou in the commercial fishery. This favorable comparison should be interpreted with reservations. First, Equation (1) was estimated from a small sample (25 observations). Second, the model is sensitive to trap costs and the method of calculating these costs is rather crude. The life span of traps varies significantly. Furthermore, maintenance costs involve removing underwater growth (traps fish better when they are clean) and onshore storage costs that vary considerably at different locations.

Influence of Relative Abundance on Soak Time and Catch per Trap Day

The catch per trap day may not reflect declining relative abundance (decreasing α in the model). As the exploitable stock declines so will the profit-maximizing soak time (Equation (20)). This reduces the number of traps each vessel can operate (given a maximum number of hauls) but increases the catch per trap day relative to what would have prevailed with the originally longer soak time. The net result is that as α declines the catch per trap day will remain constant. This can be seen by substituting Equation (20) into Equation (1).

$$\frac{L}{TD} = \frac{\alpha}{S_\pi^{\beta}} = \frac{\alpha}{\left[\left[\frac{(1-\beta)\,\rho\alpha D}{\delta}\right]^{\frac{1}{\beta}}\right]^{\beta}}$$

$$= \frac{\delta}{(1-\beta)\,\rho D}. \quad (21)$$

Equation (21) and Table 1 indicate that the measured catch per trap day will not vary with changes in the exploitable stock when the soak time also adjusts to the exploitable stock.

TABLE 1.—Catch per trap day that would be recorded with a declining stock (decreasing α) with constant (column 6) and variable (column 8) soak times.

α	β	ρ	δ	S	$L/TD = \frac{\alpha}{S^{\beta}}$	S_{π}	$L/TD = \frac{\alpha}{S_{\pi}^{\beta}}$
2.94	0.90	0.383	0.63	6.52	0.54	6.52	0.55
2.44	0.90	0.383	0.63	6.52	0.45	5.24	0.55
1.94	0.90	0.383	0.63	6.52	0.36	4.07	0.55
1.44	0.90	0.383	0.63	6.52	0.27	2.94	0.55

Adjustment of Trap Days to Include Soak Time as a Measurement of Fishing Effort

"Trap days" is customarily the recorded measurement of fishing effort. This index may not accurately reflect relative fishing effort because it only records two components of fishing effort, number of traps and number of days fished. The frequency with which traps are hauled (soak time) is not reflected. Therefore, trap days is an accurate measurement of effort only as long as soak time remains constant. According to the determinants of the profit-maximizing soak time, a constant soak time seems unlikely.

One method to adjust trap days to more accurately reflect fishing effort would be according to the relationship between the number of traps and the soak time that will achieve the same total catch. Taking the total differential of Equation (5) and setting it equal to zero:

$$dL = \frac{\partial L}{\partial S}(dS) + \frac{\partial L}{\partial T}(dT) = 0 \qquad (22)$$

$$-\beta\alpha DTS^{-(\beta+1)}(dS) + \alpha DS^{-\beta}(dT) = 0 \qquad (23)$$

$$\frac{dT}{dS} = \frac{\beta T}{S}. \qquad (24)$$

Equation (24) represents the relationship between soak time and number of traps that will result in the same total catch. This relationship can be utilized to weight trap days according to soak time. The first step is to choose a base soak time (e.g., $S = 4$). When the soak time is 4 days, then the number of "adjusted traps" is equal to the number of traps and the number of "adjusted trap days" is equal to the number of trap days.

$$T^* = T - \int_4^x \frac{\beta T}{S}(dS) \qquad (25)$$

$$T^* = T + \beta T(\ln 4 - \ln x) \qquad (26)$$

$$T^*D = [T + \beta T(\ln 4 - \ln x)]D \qquad (27)$$

where T = number of traps
4 = numeraire soak time
x = prevailing soak time
T^* = adjusted number of traps
D = fishing days
T^*D = adjusted number of trap days.

When the prevailing soak time (x) differs significantly from the base soak time (4), the integration of the interval can be more accurately estimated by:

$$T^* = T \pm \sum_{S=4}^{x} \frac{\beta T}{S} \qquad (28)$$

$$T^*D = T \pm \sum_{S=4}^{x} \frac{\beta T}{S} D \qquad (29)$$

where $x > 4 \Rightarrow \sum_{S=4}^{x} \frac{\beta T}{S} < 0$

$$x < 4 \Rightarrow \sum_{S=4}^{x} \frac{\beta T}{S} > 0.$$

Utilizing Equations (28) and (29) and 1962 parameters, Table 2 indicates how the number of traps, trap days, adjusted traps, and adjusted trap days would compare with alternative soak times.

The interpretation of Table 2 is that the adjusted number of traps (column 5) reflects the relative fishing power of a trap at different soak times. Utilizing a 4-day soak time as a base, a trap hauled every day has 2.75 the fishing power of a trap hauled every 4 days. In the other direction, a trap hauled every 7 days has 0.54 the fishing power of a trap hauled every 4 days.

TABLE 2.—Traps, trap days, adjusted traps, adjusted trap days according to alternative soak times (base: $S = 4$).

No. traps (T)	Fishing days (D)	Trap days (TD)	Soak time (S)	Adjusted no. traps (T^*)	Adjusted no. trap days (T^*D)
1	30	30	1	2.75	82.5
1	30	30	2	1.85	55.5
1	30	30	3	1.30	39.0
1	30	30	4	1.00	30.0
1	30	30	5	0.82	24.6
1	30	30	6	0.67	20.1
1	30	30	7	0.54	16.2

Adjustment of Catch Per Trap Day to a Standardized Soak Time

Once the catch per trap day has been empirically estimated with respect to the soak time

(Equation (1)), then Equation (1) can be used to easily estimate the catch per trap day that would prevail at a standardized soak time. Comparing catch per trap day at a standardized soak time will provide a more accurate measurement of relative abundance. The relative fishing power of a trap as estimated by Equation (1) yields the same results as the computations of adjusted traps in Table 2, column 5.

Conclusions

When the soak time is variable in trap fisheries, trap days may not be an accurate index of fishing effort. Furthermore, there is evidence that as the exploitable stock declines the profit-maximizing soak time declines, which can result in a measured catch per trap day that will not reflect the declining relative abundance. It is possible to adjust trap days or catch per trap day according to the soak time to more accurately reflect fishing effort (catch per unit of effort). The calibration of this adjustment requires data on the relationship between the catch and soak time. It is recommended that in the future soak time be documented to facilitate this calibration.

Acknowledgments

Data collected by R. E. Warner, University of Florida Cooperative Extension Service, Key West, on trap fishing in the Florida Keys and D. Simmons, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, on Bahama trap fishing were helpful. D. Simmons also provided review and recommendations in developing the model.

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SPECIES COMPOSITION AND RELATIVE ABUNDANCE OF LARVAL AND POST-LARVAL FISHES IN THE COLUMBIA RIVER ESTUARY, 1973

Few ichthyoplankton surveys of northern Pacific coast estuaries exist: Waldron (1972) and Blackburn (1973) surveyed larvae in northern Puget Sound; Eldridge and Bryan (1972) conducted a 1-yr survey in Humboldt Bay, Calif.; Pearcy and Myers (1974) conducted an 11-yr survey in Yaquina Bay, Oreg. No data on ichthyoplankton are available for the Columbia River estuary.

In 1973, the National Marine Fisheries Service conducted a survey of zooplankton in the Columbia River estuary to study productivity and seasonal variation of zooplankton populations. The survey also captured larval and post-larval fishes. This paper reports species composition, size range, and seasonal and horizontal occurrence of larval and post-larval fishes within the Columbia River estuary. Substrate was provided for egg deposition as an additional technique to determine if spawning was occurring in the estuary. Such investigations are valuable to assessing the importance of the estuary as a spawning and nursery ground.

Methods

Seven stations from the Columbia River's mouth to Tongue Point upstream 29 km were sampled once a month with a 0.5-m plankton net January to December 1973 (Figure 1). A single station was sampled monthly from March to

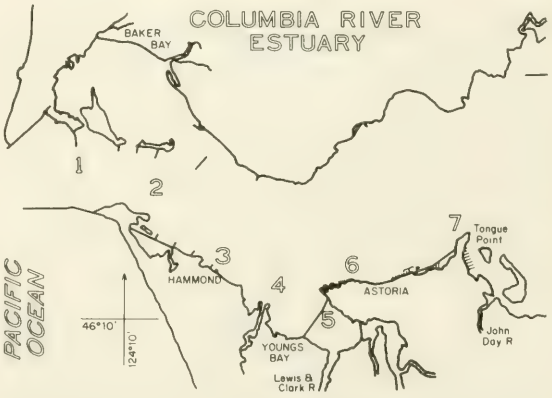

FIGURE 1.—Columbia River estuary, showing location of sampling stations.

December 1973 with a 0.9-m Isaacs-Kidd Midwater Trawl. Stations were located in channel areas where depths ranged from 12 to 26 m, with the exception of station 5 which had a maximum depth of 4.8 m.

A Coast Guard utility boat (12.3 m long) converted for research was used to sample stations during daylight at high tide. The 0.5-m net with 0.24-mm mesh was towed for 9 min at each station bottom to surface using a 3-stepped oblique tow (3 min at each level). Volume of water strained was estimated by a centrally located TSK[1] flowmeter. The 0.9-m trawl was towed once a month for 15 min at station 2 March through December 1973. The trawl was towed in a 3-stepped oblique manner (5 min at each level), surface to bottom.

Samples were preserved immediately on board the vessel with 10% Formalin in seawater. In the laboratory larvae were measured using a dissecting microscope having a micrometer eyepiece. Measurements refer to standard lengths measured from snout tip to notochord tip; after formation of the caudal fin, to the end of the hypural plate. Salinities and temperatures were recorded on the bottom and at the surface at each station with a Beckman model RS5-3 induction salinometer.

Evergreen boughs were provided as spawning substrate January through July. A small trap constructed of hardware cloth was attached to the boughs to capture and identify fishes depositing eggs. The device was operated with a hand winch mounted on a pier near station 3 and examined three times per week.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results and Discussion

Species Composition

Larvae, postlarvae, and juvenile fishes from 13 families were captured during this investigation

TABLE 1.—Checklist of larval, post-larval, and juvenile fishes captured with a 0.5-m plankton net and a 0.9-m Isaacs-Kidd Midwater Trawl during 1973.

Family, scientific, and common names	Station captured	Size range (mm)	Total number	Month collected
Clupeidae:				
Clupea harengus pallasi, Pacific herring	1, 2, 3, 4, 6	10-40	15	Mar., May, June
Alosa sapidissima, American shad	2	44	1	Aug.
Engraulidae:				
Engraulis mordax, northern anchovy	1, 2, 3	22-68	21	Jan., Mar., Oct., Nov.
Osmeridae:				
Spirinchus thaleichthys, longfin smelt	1, 2, 3, 4, 5, 6, 7	6-64	1,959	Jan., June, Oct.-Dec.
Thaleichthys pacificus, eulachon	1, 2, 3, 4, 5, 6, 7	5-8	558	Feb.-May
Allosmerus elongatus, whitebait smelt	1, 2, 3, 4	45-58	27	Oct.-Jan.
Hypomesus pretiosus, surf smelt	1, 2	36-53	27	Jan.-Mar.
Undetermined spp.	1	10-30	34	Dec.-Mar.
Gadidae:				
Microgadus proximus, Pacific tomcod	1, 2, 3	5-61	4	Mar., June, July
Stichaeidae:				
Lumpenus sagitta, snake prickleback	2, 4	13-16	5	Jan.-Feb.
Pholidae:				
Pholis ornata, saddleback gunnel	1	18-20	4	Mar.
Ammodytidae:				
Ammodytes hexapterus, Pacific sand lance	1, 2	10-16	12	Mar.-Apr.
Scorpaenidae:				
Sebastes melanops, black rockfish	3	55-67	3	July
Sebastes spp.	1, 3	5	3	Jan.
Hexagrammidae:				
Ophiodon elongatus, lingcod	2	9,12	2	Feb.-Mar.
Hexagragrammos sp.	1	6,10	2	Jan.-Feb.
Cottidae:				
Leptocottus armatus, Pacific staghorn sculpin	1, 2, 3, 6	6-13	6	Jan.-Mar., May-Sept.
Enophrys bison, buffalo sculpin	1	5, 8	2	Feb.
Cottus asper, prickly sculpin	1, 2, 3, 4, 5, 7	6-12	204	Apr.-June
Hemilepidotus spinosus, brown Irish lord	2	32	1	Mar.
Oligocottus maculosus, tidepool sculpin	1	4-8	2	Jan.
Undetermined spp.	1	6-15	3	Jan.-Feb., June
Agonidae:				
Stellerina xyosterna, pricklebreast poacher	4	7-9	3	Feb.-Apr.
Cyclopteridae:				
Liparis rutteri, ringtail snailfish	1	12-32	3	Jan., Mar.-Apr.
Liparis puchellus, showy snailfish	2	18	1	June
Undetermined spp.	1, 2	3	2	Jan.-Mar.
Pleuronectidae:				
Psettichthys melanostictus, sand sole	1	28-34	3	June
Parophrys vetulus, English sole	1, 2, 3, 4	4-21	22	Jan.-Apr., Dec.
Isopsetta isolepis, butter sole	1, 2, 3, 4	4-7	7	Jan.-Apr.

(Table 1). A total of 2,152 larvae and postlarvae were taken in 84 tows with the 0.5-m net and 784 postlarvae and juveniles were captured in 10 tows with the 0.9-m trawl.

Early stages of 22 species were taken with the 0.5-m net. The catch was dominated numerically by the Osmeridae which accounted for 89% of the total. *Spirinchus thaleichthys* were the most numerous—composing 67% of the total catch. *Thaleichthys pacificus* represented 19% of the total. *Cottus asper* made up 7% of the total and each of the remaining individual species accounted for less than 1%.

Twelve species were captured with the trawl at Station 2. *Spirinchus thaleichthys,* 22-64 mm, composed 92% of the catch. Post-larval *Hypomesus pretiosus, Allosmerus elongatus,* and juvenile *Engraulis mordax* represented the majority of the remaining total. The trawl captured three species not taken with the 0.5-m net: *Ophiodon elongatus, Hemilepidotus hemilepidotus,* and *Alosa sapidissima.*

Species composition of ichthyoplankton in the Columbia River estuary differed from that found in other northwest estuaries. Waldron (1972) and Blackburn (1973) found larval Gadidae dominated catches in Puget Sound. In Humboldt Bay, Eldridge and Bryan (1972) reported 82% of the total catch was *Clupea harengus pallasi* and *Lepidogobius lepidus.* In Yaquina Bay, Pearcy and Myers (1974) reported this combination of species was 90% of the catch. *Clupea h. pallasi* in the Columbia River estuary composed less than 1% of the total and no *L. lepidus* were captured.

Seasonal Abundance

Larval and post-larval fishes were most abundant January through May. During the summer no larval or post-larval stages were taken at any of the seven stations. Similar findings were reported in Humboldt Bay (Eldridge and Bryan 1972) and in Yaquina Bay (Pearcy and Myers 1974).

Abundance estimates are based on average monthly catches at all stations with the 0.5-m net (Figure 2). A peak of 1.1/m^3 occurred in March, primarily the result of an influx of newly hatched *Spirinchus thaleichthys*. A maximum average catch of 1.5/m^3 occurred in May, the result of an increased number of *Thaleichthys pacificus* and *Cottus asper*. Maximum catch during the year was 4.0/m^3 and occurred at station 2 in May. The

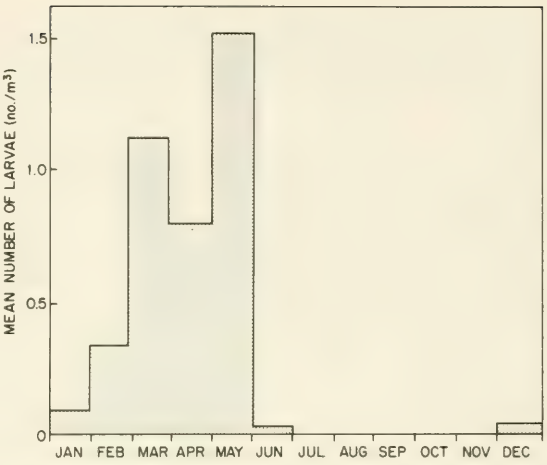

FIGURE 2.—Seasonal density of ichthyoplankton at seven locations in the Columbia River estuary during 1973. These results show average catch at seven stations with the 0.5-m plankton net.

composition was entirely *S. thaleichthys, T. pacificus,* and *C. asper.*

Juveniles were the only stage captured with the trawl from summer through fall. Those captured were: *Microgadus proximus* (60-61 mm), *Sebastes melanops* (55-67 mm), *Alosa sapidissima* (44 mm), *Leptocottus armatus* (11-13 mm), *Allosmerus elongatus* (49-58 mm), *Engraulis mordax* (45-68 mm), and *Spirinchus thaleichthys* (45-64 mm).

Horizontal Variation

The greatest variety of species was captured at stations nearer the mouth where salinities were higher. Large variations in tides and river flow combine to create a fluctuating horizontal saline intrusion; salinity is dissipated upstream and station 7, except during reduced river flow in the fall, is essentially fresh water (Haertel and Osterberg 1967 and Misitano 1974). The reduction in salinity upstream was reflected by a corresponding decrease in the variety of species (Figure 3). At station 1 there were 22 identifiable species and at stations 5 and 7 three species: *S. thaleichthys, T. pacificus,* and *C. asper.* Stations 5, 6, and 7, which exhibited similarly reduced salinities, accounted for 47.8% of the total larvae captured in the estuary with the 0.5-m net. This high percentage is due to the influx of the two species of osmerid larvae entering the estuary during the first part of the year.

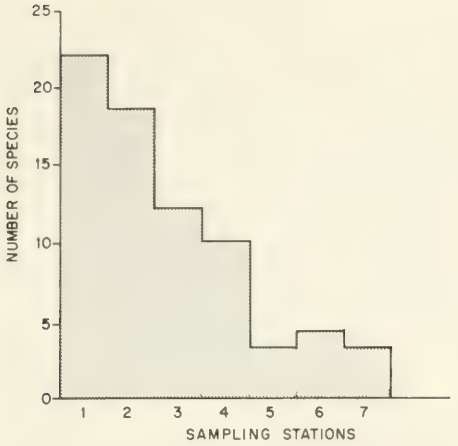

FIGURE 3.—Number of species of larval, post-larval, and juvenile fishes collected at each station in the Columbia River estuary during 1973.

Spawning on Provided Substrate

Evergreen boughs placed in the water attracted two species to deposit eggs, *Clupea harengus pallasi* and unidentified snailfish (Cyclopteridae). Thirty-three ripe adult *C. h. pallasi,* 163 mm average length, were trapped 10 April through 17 July confirming identification of the eggs. Light spawning was first observed on the boughs 10 April; moderate deposition 1-3 July. Ova were viable, eyed eggs were observed.

Adult snailfish began entering the trap 13 February. Eggs were deposited on boughs 12 and 26 February. Eggs were viable and emergent larvae were observed. Fifteen gravid adults were captured 13 February through 3 March. This snailfish has some characteristics in common with *Liparis rutteri,* which is also present in the estuary. The unknown snailfish has been closely examined and is now considered to be an undescribed species by Carl Bond at Oregon State University, Corvallis, Oreg.

Gravid adults of two species of Cottidae were captured by trapping. Ripe *Leptocottus armatus* were taken 18 February and 19 March but no spawning was observed. Jones (1962) found egg survival for this species optimum at 10-15% indicating a probably spawning population in the Columbia River estuary. Ripe *Cottus asper* were trapped 26 March, 4 and 9 April. This cottid's newly hatched larvae, as described by Stein (1972), was the third most abundant species in the estuarine ichthyoplankton. Krejsa (1967) noted that coastal populations of this cottid migrate downstream to spawn in brackish water. The capture of ripe adults and large numbers of newly hatched larvae verifies spawning of *C. asper* in the estuary.

Utilization of the Estuary

Data obtained from this investigation indicated four species, *Clupea harengus pallasi, Cottus asper, Leptocottus armatus,* and a new species of snailfish, utilized the Columbia River estuary for spawning in 1973. The greatest number of species was captured near the mouth suggesting most species are oceanic in origin.

Spirinchus thaleichthys, the most numerous species, was captured at all stations. This anadromous osmerid was reported by Hart (1973) to spawn in streams near the sea. The presence of newly hatched larvae, as described by Dryfoos (1965), confirms the presence of a spawning population in the lower Columbia system. The capture of early stages almost the year round indicates a major importance of the estuary to this species.

Thaleichthys pacificus is also an anadromous osmerid in the Columbia River. Some mainstream spawning occurs, but the majority of the run spawns in the Cowlitz River, a tributary 109 km upstream (Smith and Saalfeld 1955). Although large numbers of larvae were captured February to May, they were yolk bearing stages, 6-8 mm, indicating a downstream drift through the estuary to the ocean soon after hatching. Similar findings were reported by Larkin and Ricker (1964).

No evidence of estuarine spawning by pleuronectids was indicated. Although the upper estuary is a nursery for juvenile *Platichthys stellatus* (Haertel and Osterberg 1967), no larvae or postlarvae of this species were captured. Pearcy and Myers (1974) captured only three larvae in 11 yr in Yaquina Bay, indicating entry into the estuary is accomplished after metamorphosis. *Parophrys vetulus* were captured at two size ranges: 4-6 mm and 20-21 mm. Information from other estuaries (Pearcy and Myers 1974; Misitano 1976) indicates young *P. vetulus* enter estuarine nurseries after completion of metamorphosis.

Isopsetta isolepis utilizes the Columbia River estuary as a nursery. The National Marine Fisheries Service conducted a bottom trawling survey in the estuary from March 1973 to June 1974 (J. T. Durkin pers. commun.). *Parophrys*

vetulus, 85-165 mm, and *I. isolepis,* 95-155 mm, were commonly captured. *Isopsetta isolepis,* 4-7 mm, were captured with 0.5-m plankton net. No later stages were taken. Richardson (1973) took this species (12-22 mm) off Oregon close to shore. Entry into the estuary probably occurs as metamorphosed juveniles.

Several types of sampling equipment should be utilized in future studies to capture early stages near bottom, on tide flats, in embayments, and during darkness. This preliminary investigation indicated little spawning occurred in this west coast estuary; most species captured were spawned in the ocean, or were anadromous species that spawned upstream and drifted into the estuary. Results of this investigation and bottom trawling by other researchers indicated this estuary is utilized primarily as a nursery grounds by the post-larval and juvenile stages of several species.

Acknowledgments

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223-230

A NOTE ON: "VELOCITY AND TRANSPORT OF THE ANTILLES CURRENT NORTHEAST OF THE BAHAMA ISLANDS"

Interest of fishery scientists in the Antilles Current east of the Bahama Islands stems from a generally accepted hypothesis that it served as a conveyor of larvae of large pelagic fishes northward into the Gulf Stream system. Larvae of billfishes (Istiophoridae) were captured in plankton tows east of the Bahamas during the first MARMAP Operational Test Phase (OPT-I) cruise in July-August 1972.[1] These captures clearly

[1]Richards, W. J., J. W. Jossi, and T. W. McKenney. Interim report on the distribution and abundance of tuna and billfish larvae collected during MARMAP Operational Test Phase cruises I and II, 1972-1973. MARMAP Contrib. 16. Unpubl. manuscr., 15 p.

show that adult billfishes had been in the area shortly before the sampling occurred, but the implication of the transport of the larvae northward by the Antilles Current is not so clear. We have reason to doubt the existence of the strong, steady, broad surface flow to the northwest which has been assumed to be characteristic of the Antilles Current east of the northern Bahamas.

In a recent analysis of six occupations of Standard Section A-7 (Figure 1) by U.S. Coast Guard cutters, Ingham (1975) did not find a strong, steady, broad surface flow attributed to the Antilles Current (Wüst 1924; Boisvert 1967). In a study of directly measured values of the transport of the Gulf Stream between the Florida Straits and Cape Hatteras, Knauss (1969) noted that the transport increases at a rate of about 7%/100 km, from 33×10^6 m^3/s in the Florida Straits, to 63×10^6 m^3/s off Cape Hatteras. Increases of this magnitude were also evident in earlier transport measurements for the Florida Straits (Wüst 1924; Montgomery 1941) and Cape Hatteras (Iselin 1936). Exactly how this increase takes place has not been determined. Wüst (1924) and Iselin (1936) felt that the Antilles Current makes a significant addition (12×10^6 m^3/s) to the Gulf Stream just north of the Bahama Islands, but Stommel (1965) felt that this value for the contribution of the Antilles Current was questionable. It should be noted that Wüst's (1924) transport to the northwest was approximately balanced by two countercurrents on each side of the current moving to the southeast.

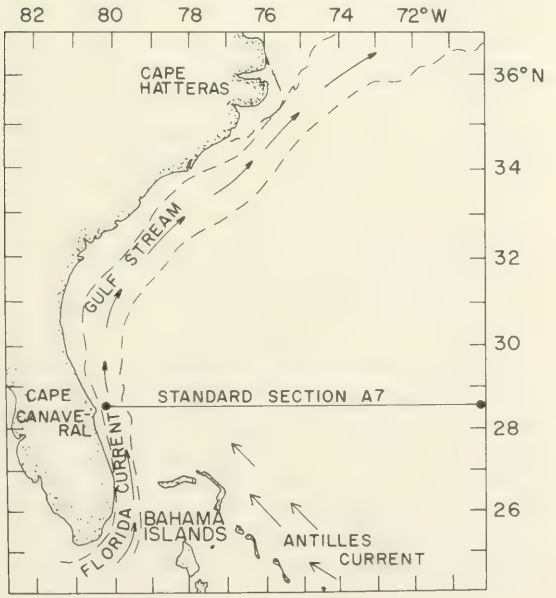

FIGURE 1.—Position of Coast Guard Standard Section A-7 in relationship to surrounding currents and land masses.

The geostrophic velocities and volume transports (Table 1) obtained by Ingham (1975) indicate that the previous estimate (Wüst 1924) of the transport of the Antilles Current is too large and that a better estimate of the mean northward transport is on the order of 8.6×10^6 m^3/s. The difference in reference levels between Ingham (1,000 decibars) and Wüst (800 decibars) does not account for this discrepancy since Wüst's shallower reference level would result in less transport than Ingham, not more. In the six transects measured by Ingham only one showed a net transport large enough to account for the above mentioned increase in the Gulf Stream. In addition, the net transport through the section was highly variable, showing values of 3.4 and 6.4×10^6 m^3/s southward in two of the transects. Ingham (1975) suggested that some mechanism other than the Antilles Current may account for the increase in the Gulf Stream and that the contribution of local wind-driven (Ekman) transport be considered as a possibility, since the mean direction of the winds in the vicinity would produce a northward or northwestward drift.

In order to determine this northward transport contribution by locally wind-driven currents, quarterly averages (January-March, April-June, etc.) of Ekman transport values for 1946-73 were obtained from the Pacific Environmental Group, National Marine Fisheries Service, NOAA for three locations northeast of the Bahama Islands, along lat. 27°N at long. 78°W, 75°W, and 72°W (Figure 1). These values were calculated from the mean monthly atmospheric pressure field using the method described by Bakun (1973) to determine the mean monthly wind stress on the ocean surface and the resulting Ekman transport. The quarterly mean meridional Ekman transports, per unit length, for each position were averaged to give a mean transport value for a hypothetical

TABLE 1.—Transports across Coast Guard Standard Section A-7 as reported by Ingham (1975).

Date of transect	Transport (10^6 m^3/s) and direction
29-30 Jan. 1967	16.0 North
26-28 June 1967	30.4 North
24-25 June 1968	3.4 South
9-11 Dec. 1969	3.9 North
29 Sept.- 1 Oct. 1970	6.4 South
17-19 Nov. 1970	11.4 North

transect along lat. 27°N. This value was then multiplied by the length of the transect to give a net quarterly meridional transport through the transect. The hypothetical transect extends eastward from the Bahama Islands, 668 km, to the same longitude as the eastern end of Standard Section A-7 (about long. 70°12′W). Thus it crosses the same portion of the Antilles Current as that cut by Standard Section A-7, but about 180 km upstream of it. Therefore, meridional Ekman transports computed for the transect along lat. 27°N can be compared with measured geostrophic transports through A-7. Although the effects of lateral boundaries were not considered, the piling up of water against the Bahama Banks would result in a southeastward geostrophic flow, further substantiating the result of this report.

The results of these computations, for this hypothetical transect, show a large range of net quarterly meridional Ekman transport values, from 60×10^3 m^3/s northward to 20×10^3 m^3/s southward with an overall mean of net transports, over 28 yr, of $15\pm2\times10^3$ m^3/s northward (the range gives the limits of the 95% confidence level) and an SD of 11×10^3 m^3/s. When the 28 yr of net meridional transports were averaged by quarters, there was the appearance of distinct seasonality, with the lowest average value in the first quarter (January-March) amounting to $7\pm4\times10^3$ m^3/s northward with an SD of 12×10^3 m^3/s. The transport increased in the second (April-June) and third (July-September) quarters to 15 ± 3 and $17\pm2\times10^3$ m^3/s northward with respective SD's of 9 and 6×10^3 m^3/s. The fourth quarter (October-December) had the highest value of $23\pm4\times10^3$ m^3/s northward, with an SD of 12×10^3 m^3/s. These values for the Ekman transport are three orders of magnitude too small to account for the transport increase in the Gulf Stream. Thus locally induced Ekman drift can be ruled out as a significant contributor.

There still is a possibility that an Antilles Current could account for the observed increase in transport of the Gulf Stream. If a strong, narrow band of the current hugged the eastern edge of the Bahama Banks and joined the Gulf Stream before it crossed Standard Section A-7 (Figure 1), it would have escaped detection in Ingham's (1975) analysis. The existence of such an intense current would contradict Knauss' (1969) observation that the transport increase in the Gulf Stream takes place gradually from the Florida Straits to Cape Hatteras, with no large increase in transport ($>2\times10^6$ m^3/s) south of lat. 32°N and the suggestion by Worthington (in press) and Sturges (1968) that the increase in transport of the Gulf Stream takes place over its entire length and at all levels. Nevertheless a study in preparation by R. Yager (pers. commun.) using direct transport measurements appears to show a narrow (80 km), intense (12×10^6 m^3/s) current to the northwest hugging the east side of the Bahama Banks.

A measure of the significance of Ekman transport in moving the larvae of pelagic fishes northward to the Gulf Stream can be obtained by deriving a rough estimate of the average speed of neutrally buoyant objects in the wind-driven layer. For this the average northward transport is divided by the area of the cross-section through which the flow is occurring (depth of layer × length of section). Using the familiar empirical relationship,

$$D = \frac{7.6W}{\sqrt{\sin\phi}} \quad \text{(Defant 1961 Vol. I:422),}$$

where D is the depth of the wind-influenced layer, W is the wind speed (here the median wind speed, 5.5 m/s shown for lat. 25°-30°N, long. 70°-75°W in the U.S. Naval Oceanographic Office atlas 1963), and ϕ is the latitude, we obtain an estimate of the average depth of the wind-influenced layer to be about 60 m. From the depth (60 m), the length of the section (668 km), and the net transport computed earlier ($15\pm2\times10^3$ m^3/s), we obtain an estimate of the average northward velocity of larvae to be 0.04 cm/s. It is apparent that this velocity, which translates to 0.03 km/day, is considerably smaller than the geostrophic velocities through lat. 28°35′N reported by Ingham (1975) which generally ranged from 5 to 40 cm/s either northward or southward.

The vertical distribution of ichthyoplankton could have a considerable effect on their transport by wind-driven currents; however, their vertical distribution is not well known. If, in order to obtain a maximum possible velocity, we assume that the larvae remain in the upper meter or so of the wind-driven layer instead of spending time at various depths throughout it, then their wind-driven drift speed would be considerably greater than the 0.04 cm/s average. Using the relationship

$$V_0 = \frac{\lambda W}{\sqrt{\sin\phi}} \quad \text{(Defant 1961 Vol. I:418),}$$

which relates surface current speed (V_0) to wind speed (W) in terms of latitude (ϕ) and an empirical constant ($\lambda \doteq 10^{-2}$), we obtain an estimate of average wind-driven surface current velocity of 5.7 cm/s northward.

In light of the velocity estimates, it is apparent that locally wind-driven currents are significant for the northward transport of pelagic larvae east of the northern Bahamas only if the larvae spend most of their time near the sea surface. If, instead, they are scattered throughout the upper layer or undergo diurnal vertical migration, their northward progress will be much slower.

Another possible pathway of larval transport which should be considered, however, is the nearshore band of strong flow mentioned by R. Yager (pers. commun.). If such a band exists as a regular, steady feature of the current field east of the Bahama Banks, then it would be particularly informative to conduct seasonal ichthyoplankton surveys on a scale appropriate to determine the relative abundance of pelagic larvae in and near the current band.

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SALINITY ACCLIMATION IN THE SOFT-SHELL CLAM, *MYA ARENARIA*

A steady increase in sewage pollution followed by the closing of many productive shellfish growing areas has seriously affected the harvesting of the soft-shell clam, *Mya arenaria,* in the State of Maine. In areas where a large percentage of the population derives its income from harvesting soft-shell clams, these closings have caused severe economic hardships. Beginning in the mid-1950's the Maine Department of Marine Resources (then Maine Department of Sea and Shore Fisheries) accelerated research on clam depuration in an attempt to salvage moderately polluted clams of 70-700 most probable number of *Escherichia coli* bacteria per 100 g. Based upon the design and development of a pilot process (Goggins et al. 1964) five commercial depuration plants have been established. The first of these (Seafair, Inc.[1]), in Phippsburg, Maine, utilized clams dug from Parker Head, Maine. During routine operation of this plant, it was apparent that exposure of clams to certain salinity and temperature conditions increased the time required for depuration.

Former investigators have revealed that pumping activity and associated shell and ciliary movements are affected when bivalves other than soft-shell clams are immersed in water of a different salinity from that to which they are accustomed (Wells et al. 1940; Medcof 1944; Loosanoff[2]). In this paper, salinities lower than

[1]Reference to a commercial enterprise does not imply endorsement by the National Marine Fisheries Service, NOAA.

[2]Loosanoff, V. L. 1952. Behavior of oysters in water of low salinities. Conv. Address Proc. Natl. Shellfish. Assoc., Atlantic City.

the accustomed are called "dilutions," those above, "concentrations." The literature shows that the effects of dilution upon *Mya arenaria* are most noticeable when reduced to the stress point. The stress point for Massachusetts clams is approximately 15‰ (Matthiessen 1960), 22-24‰ for Medomac River, Maine, clams (Welch and Lewis[3]) and 5‰ for Chesapeake Bay clams (Schubel[4]).

Pumping activity and associated feeding and ciliary movements of many bivalves are also known to be directly affected by temperature changes (Nelson 1923; Gray 1924; Galtsoff 1928; Hopkins 1931, 1933; Elsey 1936; Loosanoff 1939, 1950, 1958; Harrigan 1956; Goggins et al. 1964; Feng[5]).

To our knowledge, only Loosanoff (see footnote 2) and Welch and Lewis (see footnote 3) have attempted to relate changes in bivalve behavior to changes in both salinity and temperature.

This investigation was undertaken to establish the relationship of temperature to acclimation time when *Mya* is immersed into dilutions and concentrations of seawater. The results are applicable to many real situations where *Mya* are harvested from an area with one set of environmental conditions and subjected to acclimation and depuration in an area of another.

Materials and Methods

Salinity Control Apparatus

The constant flow apparatus used in the following experiments was similar in principle to that used by Loosanoff and Smith (1950). The complete system consists of freshwater and saltwater constant head reservoirs and nine adjustable head units, four regulating the freshwater flow and five the seawater flow. Water from each adjustable head or pair of heads flowed through plastic tubing into the bottom of a large mixing tube and then into the test tank. In this manner, ambient salinity and four dilutions could be maintained simultaneously. Temperature differences between the freshwater and saltwater constant head reservoirs were eliminated by the installation of a temperature equalizer functioning on the heat exchanger principle.

Experimental Design

Clams were dug by commercial clam diggers (under Department of Marine Resources supervision) from moderately polluted clam flats at Parker Head, Maine, and transported to the laboratory shortly thereafter. Broken clams and clams under 50 mm were discarded, and the remaining clams were thoroughly washed and held in flowing control salinities until shell liquor salinities were the same as control salinities. The experimental temperatures desired were obtained over a 10-mo period using the natural range of ambient seawater temperature available. Approximately 1 bushel of clams was used in each set of dilution and concentration experiments testing salinity acclimation rates at ambient water temperature. Clams were acclimated to control salinities of 30.54-31.80‰ (dilution experiments) and 16.26-17.14‰ (concentration experiments) and then roughly divided into five groups; one group remained in the control salinity and the other four groups were immersed into tanks set at other dilutions and concentrations of seawater.

Changes in shell liquor salinity were chosen as the criteria for the measurement of acclimation because shell liquor was easily obtained from each group of six clams by inserting a knife into the region of the foot opening and draining the contents into a paper cup. Five milliliters of this total and a sample of tank water were analyzed for salinity by the Knudsen Method. Acclimation had occurred when shell liquor salinities were the same as tank salinities. The oxygen content of the water flowing into and out of each test tank was measured by the Azide Modification of the Iodometric Method (American Public Health Association 1967). We attempted to regulate the flow rate in each tank at approximately 1,000-1,100 ml/min. All temperature measurements were made with a calibrated glass thermometer. Measurements of salinity, temperature, and flow rate were recorded as the mean±1 SE. Appropriate curves were fit where necessary.

Results

The dissolved oxygen content of the water used

[3]Welch, W. R., and R. D. Lewis. 1965. Shell movements of *Mya arenaria*. Unpubl. manuscr., [U.S.] Bur. Commer. Fish. Biol. Lab., West Boothbay Harbor, Maine.

[4]Schubel, J. 1973. Report on the Maryland State Department of Health and Mental Hygiene cooperative study to determine cause and extent of high bacteria counts found in *Mya arenaria* in 1973. Md. Dep. Health Ment. Hyg., 57 p.

[5]Feng, S. Y. 1963. Activity of the hard clam *Mercenaria mercenaria*. Talk at Rutgers, the State University of New Jersey and NAS Meeting July (Furfari 1966).

in dilution and concentration experiments varied between 5.91 and 12.58 mg/liter depending largely upon the ambient range of temperature and salinity conditions encountered (Table 1). It is evident in Table 1 that no significant differences exist between flow rates at the beginning and end of a given group of experiments.

The results of one typical set of dilution and concentration experiments are presented in Figure 1. A comparison of this set of experiments reveals that *Mya* acclimates faster to high salinity from 17‰ than to 17‰ from high salinity. Similar observations were noted for all ambient temperature ranges used. The approximate number of hours required to acclimate to each dilution from the control was recorded for each

TABLE 1.—Parameters recorded during dilution (D) and concentration (C) experiments with *Mya arenaria* at ambient temperature ranges.

Experiment	Tank salinity (‰)	Water temp (°C)	Flow rate (ml/min) Beginning	Flow rate (ml/min) End
2.9°-3.2°C:				
D	[1]31.36±0.04			
	27.37±0.08	2.9±0.2	1,132± 94	1,184±104
	22.48±0.04			
	16.88±0.05			
	11.49±0.06			
C	31.16±0.06			
	27.41±0.10	3.2±0.2	1,170±106	1,156±115
	22.07±0.04			
	[1]16.58±0.03			
	11.58±0.12			
6.4°-6.9°C:				
D	[1]31.80±0.15			
	27.16±0.17	6.9±0.3	1,152± 71	1,156± 45
	22.35±0.07			
	16.93±0.08			
	11.91±0.13			
C	31.43±0.05			
	28.04±0.06	6.4±0.2	1,100± 66	1,064± 70
	22.65±0.12			
	[1]17.14±0.07			
	11.89±0.03			
10.0°-10.7°C:				
D	[1]30.54±0.06			
	27.15±0.11	10.0±0.2	1,109±122	1,111±112
	21.66±0.08			
	16.82±0.06			
	11.71±0.03			
C	31.18±0.07			
	28.09±0.03	10.7±0.1	1,068±123	1,084±123
	21.82±0.07			
	[1]16.26±0.11			
	12.04±0.32			
15.4°-16.3°C:				
D	[1]31.01±0.07			
	27.55±0.15	16.3±0.1	938± 75	980± 62
	22.53±0.11			
	16.95±0.06			
	12.05±0.04			
C	30.89±0.09			
	27.57±0.07	15.4±0.1	1,028± 79	957± 78
	22.95±0.14			
	[1]17.11±0.09			
	11.78±0.03			

[1]Control.

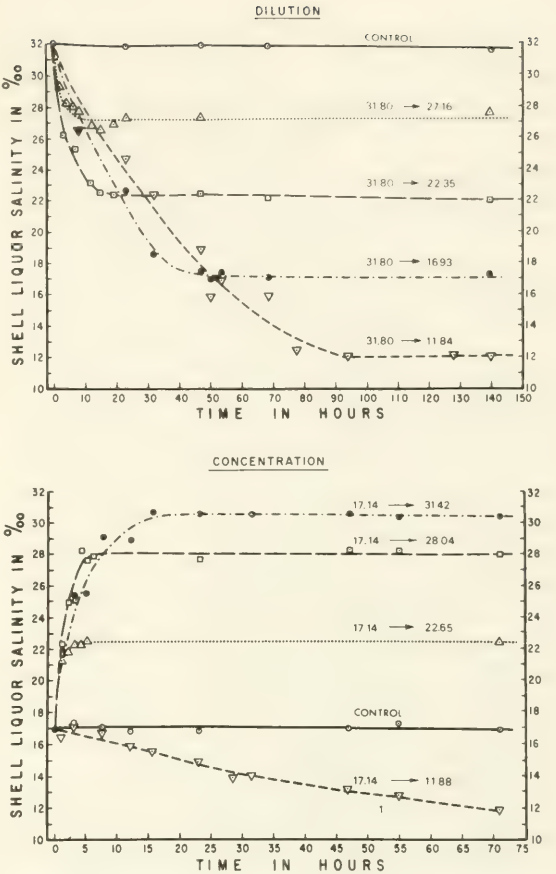

FIGURE 1.—Shell liquor salinity acclimation rates for *Mya arenaria* in dilutions and concentrations at 6.4°-6.9°C (lines fitted by eye).

ambient tempreature range used, plotted for each dilution in Figure 2, and the appropriate curve was fit. Hence at 8°C in Figure 2, 95 h are required for *Mya* to acclimate to 11.49-12.05‰ salinity from the control, 45 h to 16.82-16.95‰ from the control, 15 h to 21.66-22.53‰ from the control, and 10 h to 27.15-27.55‰ from the control. In Figure 2, a geometric relationship exists between temperature and acclimation time after immersion into various dilutions. The approximate time required to acclimate to each concentration from the control, at each ambient temperature range, was recorded in Table 2. Tested at 95% confidence intervals (±2 SE), Table 2 reveals that no significant differences exist between the mean numbers of hours required to acclimate to each concentration experiment at all temperature ranges combined. Table 2 also reveals that no significant differences exist between the mean

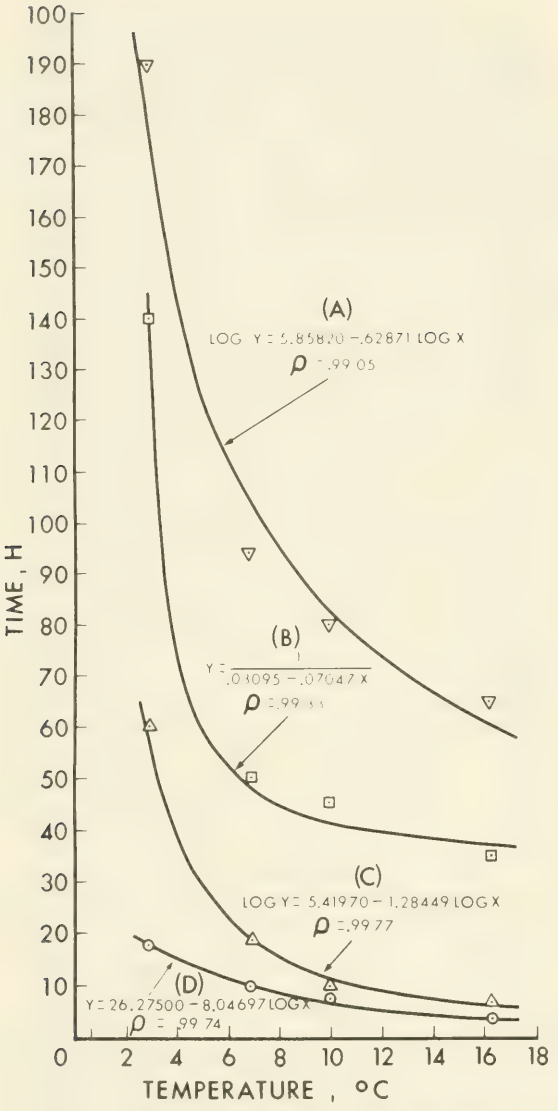

FIGURE 2.—The relationship between temperature and time required to acclimate *Mya arenaria* from the control salinity (30.54-31.80‰) to the following dilutions: (A) 11.49-12.05‰; (B) 16.82-16.95‰; (C) 21.66-22.53‰; (D) 27.15-27.55‰.

acclimation time (±2 SE) for all concentration experiments combined at each temperature range.

Discussion

A constant flow apparatus is ideally suited to shellfish studies. Continuous exchange of water assures a rapid elimination of metabolic waste products and more closely resembles natural conditions than does a standing water system

TABLE 2.—The relationship between temperature and the approximate number of hours required for *Mya arenaria* to acclimate to three concentrations from a control salinity of 16.26-17.14‰.

Temp (°C)	Control 30.89-31.43‰	Control 27.41-28.09‰	Control 21.82-22.95‰	$\bar{X}$±SE
3.2	about 10 h	about 10 h	about 7 h	9.0±1.0 h
6.4	about 20 h	about 7 h	about 5 h	10.7±4.7 h
10.7	about 8 h	about 5 h	about 4 h	5.7±1.2 h
15.4	about 8 h	about 8 h	about 6 h	7.3±0.7 h
$\bar{X}$±SE	11.5±2.9 h	7.5±1.0 h	5.5±0.6 h	

(Loosanoff and Smith 1950; Loosanoff see footnote 2).

Van Dam (1935) observed that oxygen utilization in *Mya* is independent of oxygen concentration down to about 2 cm^3/liter (2.8 mg/liter). There is therefore no reason to believe that the variations in dissolved oxygen encountered in these experiments altered the pumping activity of *Mya*.

In these studies, the exclusive use of adult *Mya* is consistent with Matthiessen's (1960) observation that adult and juvenile *Mya* have different tolerance levels to low salinity conditions.

The phenomenon of faster acclimation to concentrations than dilutions has not been previously reported for *Mya*. Loosanoff (see footnote 2), however, reported that oysters moved from 10‰ into 20-25‰ returned to normal pumping very quickly.

The relationship of pumping activity to shellfish depuration has been well documented (Furfari 1966). When shellfish are subjected to suitable salinity and temperature conditions, high pumping activity is maintained and efficient depuration results.

Furfari (1966) reported that pumping activity is reduced for a time when shellfish are subjected to salinity other than that to which they are accustomed in the harvest area. During this time, our data suggest that *Mya* periodically "samples" the water conditions and acclimates to them gradually. The length of time required is related to the magnitude of the dilution. Welch and Lewis (see footnote 3) have observed that this "sampling" behavior is performed by opening the siphons very slightly and then gently closing them, very little water having passed through the clam in the process.

Our studies indicate that water temperature directly influences the rate at which salinity acclimation occurs. The results are consistent with Harrigan (1956) who observed that the pumping rate of *Mya* increased up to a temperature of 16°-20°C and Goggins et al. (1964) who

observed that *Mya* activity (measured by physical criteria: extension of siphon, response to tactile stimuli) increased in direct proportion to an increase in temperature. Other investigators have reported that *Mya arenaria* pumps as effectively at all temperatures (Belding 1930; Marston 1931; Arcisz and Kelly 1955). If this were true in our studies, *Mya* would be expected to acclimate to a dilution as quickly at 3°C as at 16°C. Clearly, in the case of Parker Head clams, our findings do not agree with these authors.

In the case of Seafair, Inc., it is apparent that depuration took longer because the Parker Head clams first had to acclimate to unaccustomed salinity before they could actively pump and cleanse themselves. Low water temperature would, of course, tend to lengthen this acclimation period. Our findings are consistent with Furfari's (1966) statements, "Time taken by shellfish to acclimate to the stress of a change in salinity, is time lost in depuration."

In addition to establishing the time required for *Mya* to acclimate to dilutions at ambient temperature ranges, this study demonstrates the need for appraising the response of clams from the harvest area to the environmental conditions existing at the depuration site. Acclimation times recorded in this paper are specific for Parker Head clams. *Mya* dug from other locations may respond differently.

Acknowledgments

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PHOTOGRAPHIC METHOD FOR MEASURING SPACING AND DENSITY WITHIN PELAGIC FISH SCHOOLS AT SEA

Few measurements exist of the spacing and density of fish within schools in the sea (Radakov 1973) although these characters have been well-studied in the laboratory (Breder 1954; Keenleyside 1955; Dambach 1963; Williams 1964; John 1964; Cullen et al. 1965; Hunter 1966; van Olst and Hunter 1970; Symons 1971). The density and spacing of fish within schools under natural conditions must be known if realistic fish abundance estimates are to be made from sonar survey data (Hewitt et al. 1976). This note describes a camera system that photographed fish schools at sea and a method used for estimating the density and interfish spacing from the photographs.

The camera system[1] consisted of an anodized aluminum casing which housed a spring-driven advance 35-mm camera, strobe light, and electrical components. The system was made watertight by creating a vacuum which sealed the acrylic lenses to the casing. Attached to the casing were a depth release with expendable chain ballast, floats, and a signal flag (Figure 1).

Upon immersion, the camera assumed an upright position, closing a mercury switch and starting an electric timer which activated the camera shutter and strobe light simultaneously. The system took 14 photographs per drop at set intervals of 24 or 48 s while sinking at a rate of 10

[1]Designed by Daniel M. Brown, Scripps Institution of Oceanography (SIO) from an idea of John D. Isaacs, SIO. Blueprints are available at the Marine Sciences Development Shop, SIO.

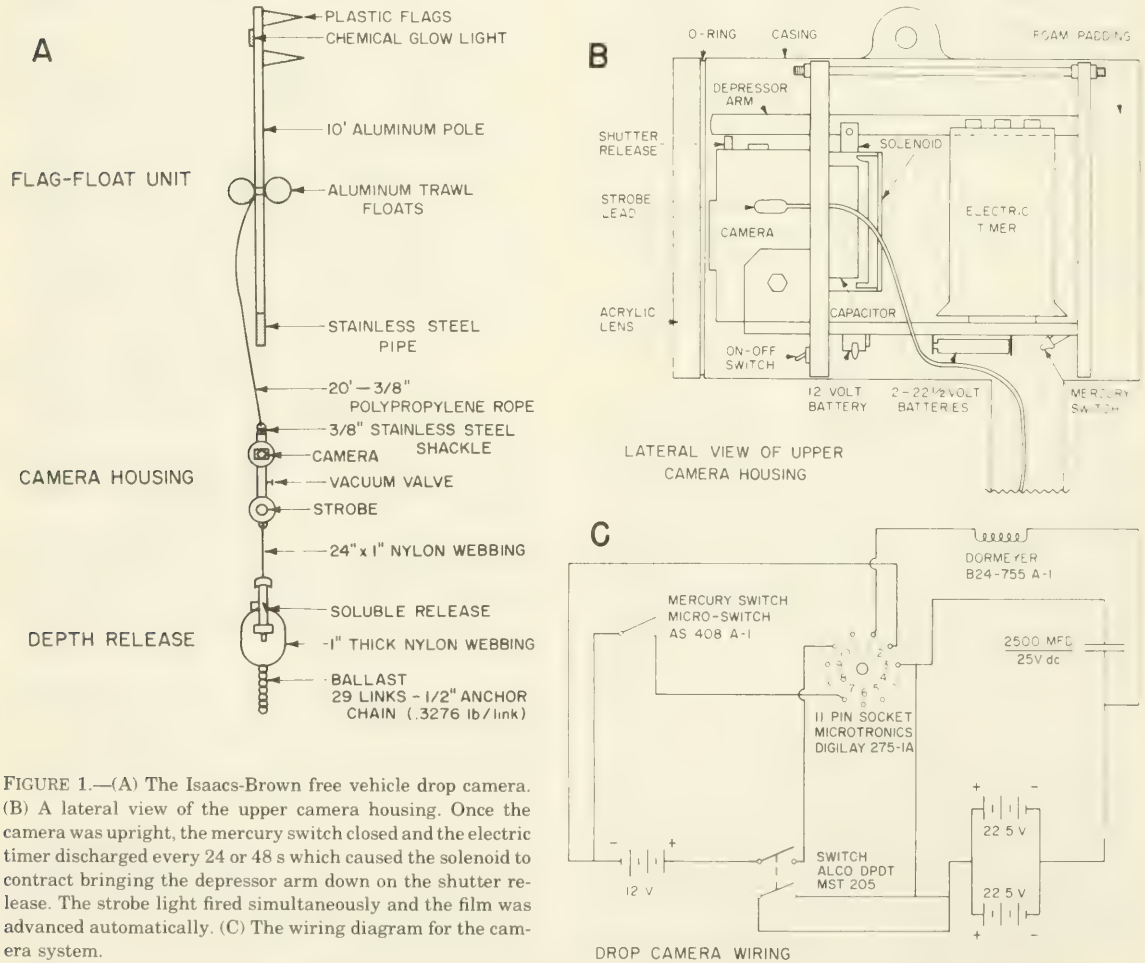

FIGURE 1.—(A) The Isaacs-Brown free vehicle drop camera. (B) A lateral view of the upper camera housing. Once the camera was upright, the mercury switch closed and the electric timer discharged every 24 or 48 s which caused the solenoid to contract bringing the depressor arm down on the shutter release. The strobe light fired simultaneously and the film was advanced automatically. (C) The wiring diagram for the camera system.

m/min. At a preset depth, the ballast was released and the system returned to the surface.

Fish lengths were measured from photographic enlargements with an x-y coordinate reader and only those fish enclosed by a circle of 6 to 10 cm in diameter, drawn centered on the photograph, were counted in order to reduce computer processing time and peripheral photographic distortion. Repeated measurements of a photograph indicated a mean error in individual body length of 3.4% and a maximum error of less than 9.0% for any individual.

To estimate the distances from the camera to the fish it was assumed that all the fish were of the same size, were all oriented perpendicularly to the camera lens, and thus the differences in fish image size were dependent only on the distance from the camera. The distance between any fish and the camera was determined by calculating the ratio of the standard fish size to the 35-mm negative image size and substituting this value into the underwater calibration equation of the camera (Figure 2). The mean standard length of 12.0 cm (s = 1.9 cm) for anchovy in southern California waters (Mais 1974) was used as the standard fish size.

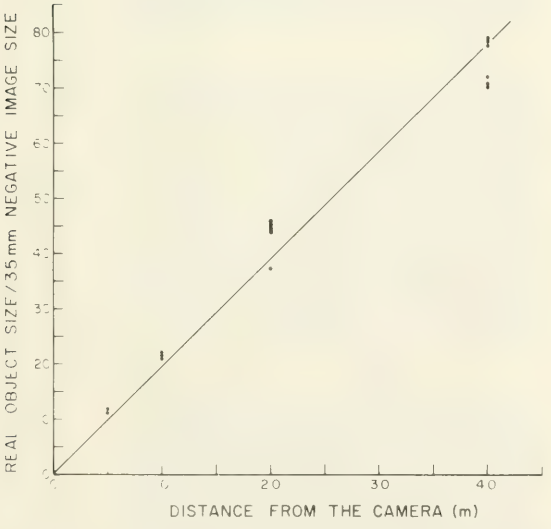

FIGURE 2.—The calibration curve for the Isaacs-Brown free vehicle drop camera. This camera system was calibrated under water by photographing objects of known sizes at fixed distances and the ratio of the real object to negative image size (y) was plotted against distance from the camera (x). The equation for the line is $y = 19.56x$. The distance to a fish was then determined by calculating the ratio of the standard fish size (12 cm) to the 35-mm negative image size of that fish.

A computer program calculated the lengths of the fish and produced a cumulative percent distribution of their sizes. One would expect the number of fish with small image sizes to increase with distance from the camera lens, but analysis revealed that a distance existed in most photographs at which the numbers of smaller fish failed to increase presumably because the more distant fish were not resolved owing to overlap, water clarity, and loss of lighting. An arbitrary limit was established at that image size by noting a change in slope on the graph of the cumulative percent distribution of fish lengths (Figure 3) and all fish smaller than the limit were not considered.

After establishing the minimum fish image size to be included in the program, a three-dimensional model of the photograph was constructed by calculating a third coordinate, z, based on fish image size and by adjusting the x and y coordinates for distance from the camera. The midpoint of each fish was then determined and a mean distance to the nearest neighbor was calculated by comparison with the midpoints of all the fish. The density of the school was computed by dividing the num-

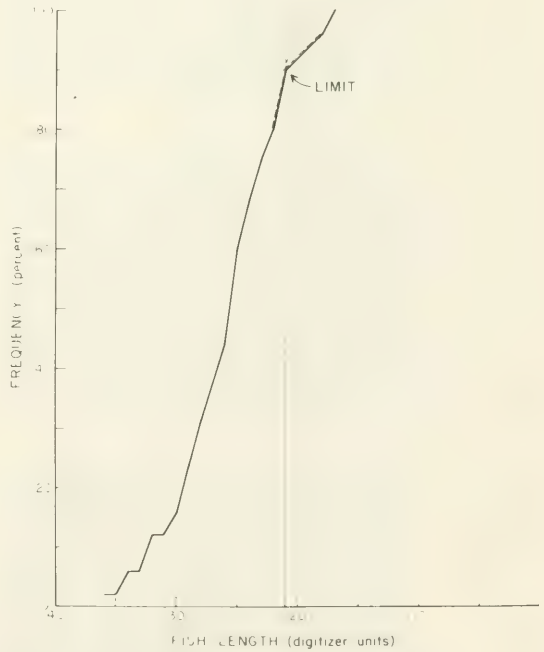

FIGURE 3.—The cumulative percent of length frequencies (in arbitrary units) for the fish measured in photograph 10 (Figure 4). Graphs of this form were made for each photograph analyzed in order to determine the distance beyond which all fish images were not resolved. The limit was made arbitrarily at the first apparent decrease in slope of the distribution.

ber of fish by the volume of the truncated cone between the planes of the largest and smallest fish image.

In September 1974, 14 camera drops were made in the Santa Barbara Channel on anchovy schools located by sonar. Observation of camera drops revealed that the slow sinking rate and $^1/_{1,000}$-s strobe flash did not disturb the fish. A space of about 4 m in diameter opened up in the school below the system as the camera descended. The increase in the school density caused by formation of the open space in the school was not detected in my analysis.

Anchovy schools appeared on 16 of the 230 photographs taken. For the 10 photographs in which the fish seemed to be perpendicular to the camera, the mean density of the school was 114.8 fish/m^3 where s = 99.1 fish/m^3 and the mean of the mean distance to the nearest neighbor was 1.2 body lengths with s = 0.3 body length (Figure 4, Table 1).

Photographs 6-10 were of the same school taken over a 10-min period. Excluding photograph 7, in which the fish appeared to be reacting to the camera or a predator and are more compact, the densities calculated for this school were 60, 56, 51, and 55 fish/m^3 with a mean distance to the nearest neighbor of 1.27, 1.28, 1.63, and 1.42 body lengths, respectively.

The interfish distances estimated for the schools photographed in this field study are, in general, larger than those reported in laboratory studies. This suggests that the small tanks used in these studies have caused fish to form more compact schools than they typically do under natural conditions.

The camera and these techniques could be of considerable value in determining the density and species composition of pelagic fish schools for sonar surveys. They should also be of value in the study of the behavior of schooling fish. School densities are known to change during feeding, predatory attack, and under diminished light intensity (Shaw 1970; Radakov 1973). Using the drop camera, it may now be possible to study the behavior of schools in the sea since interfish distance is as yet the best characteristic to measure changes in schooling tendencies.

TABLE 1.—Parameters of schooling compaction generated by the computer program for the 10 photographs in Figure 4.

Photo number	Fish/m^3	Mean distance (body lengths) to the nearest neighbor
1	100	1.24
2	174	0.84
3	78	1.38
4	50	1.35
5	366	0.79
6	60	1.27
7	158	0.86
8	56	1.28
9	51	1.63
10	55	1.42
Mean	115	1.20
Standard deviation	99	0.28

Acknowledgments

I thank Daniel M. Brown of the Scripps Institution of Oceanography for instructing me in the use of the camera; the California Department of Fish and Game for providing time on the vessel *Alaska* and the assistance of its crew; John Ford for assisting with the camera calibration; John Hunter, Paul Smith, and Roger Hewitt of the National Marine Fisheries Service for helping in various ways; and Evelyn Shaw and Charles Breder for reviewing the manuscript.

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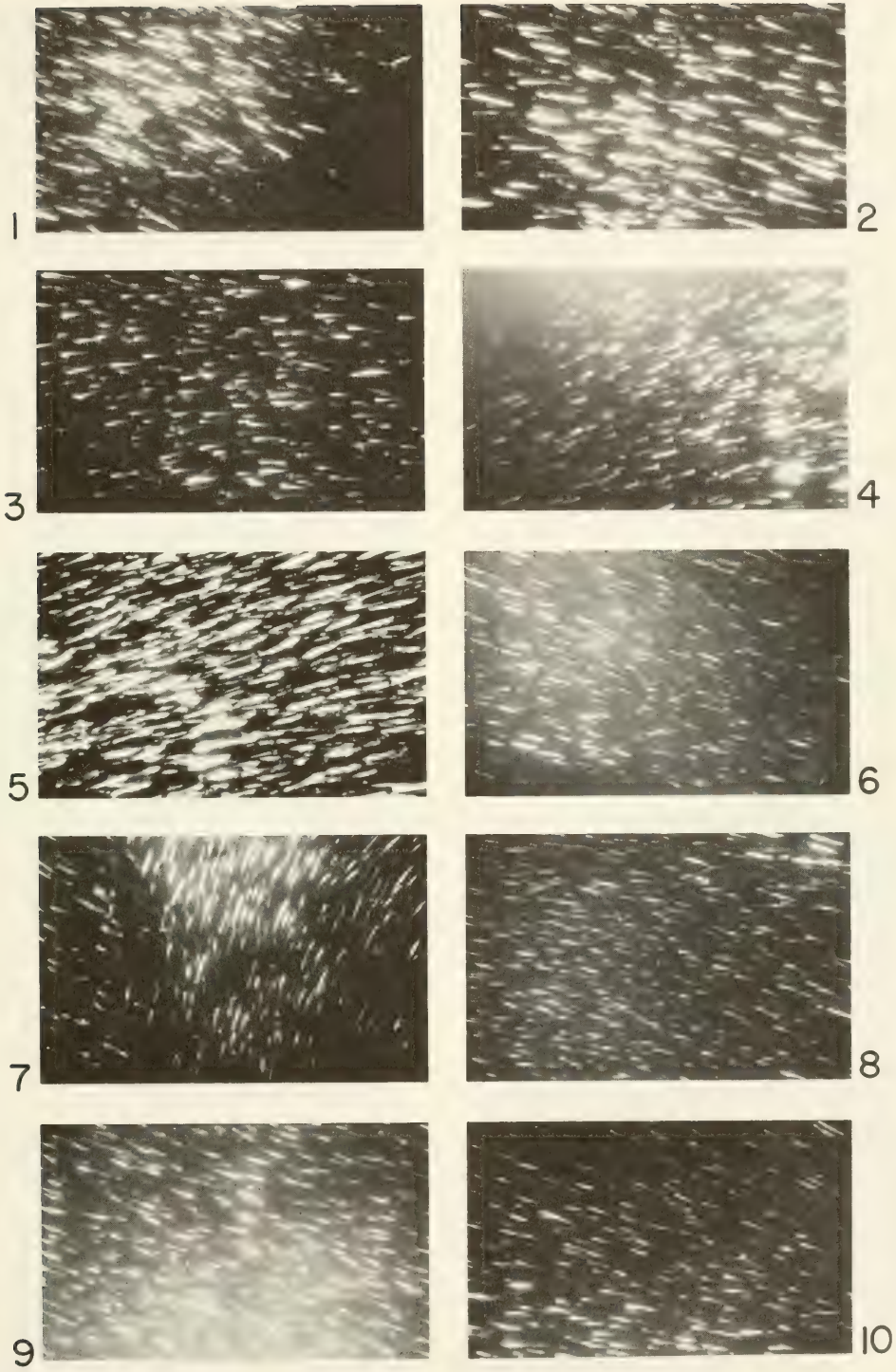

FIGURE 4.—Anchovy schools photographed in the Santa Barbara Channel with the Isaacs-Brown free vehicle drop camera during September 1974. Estimated fish density (fish/m^3) in each photograph, left to right, top row 100, 174, second row 78, 50, third row 366, 60, fourth row 158, 56, fifth row 51, 55.

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FEEDING BY ALASKA WHITEFISH, *COREGONUS NELSONI*, DURING THE SPAWNING RUN

It seems to be generally agreed that most coregonids feed but little, if at all, during their prespawning run and only minimally until spawning has taken place (Wagler 1927; Hart 1930, 1931; Birrer and Schweizer 1936; Van Oosten and Deason 1939; Slack et al. 1957; Qadri 1961; A. H. Townsend and Ray Baxter, Alaska Department of Fish and Game, pers. commun.). Coregonids are, however, known to feed, at least to some extent, during the spawning period, but we have not found any published indications of whether such feeding is pre- or post-spawning of the individual fish. Until the individual fish has at least begun to spawn, feeding is at a very low level (Wagler 1927; Hart 1930, 1931; Birrer and Schweizer 1936; Jacobsen 1974). Subsequent to spawning, feeding intensity increases greatly, apparently compensating for the loss of condition due to spawning. Coregonid and other fish eggs are often an important food item at this time (Bajkov 1930; Jacobsen 1974). The few eggs taken by presumed prespawners are probably ingested incidentally to normal respiratory movements rather than by deliberate feeding (Hart 1930).

The purpose of the present paper is to document an instance of active feeding by a coregonid species during the prespawning run.

The least cisco, *Coregonus sardinella*, and Alaska whitefish *(Coregonus nelsoni = C. clupeaformis* complex of McPhail and Lindsey 1970) of the rivers of interior Alaska exhibit highly concentrated spawning runs. In the Chatanika River, near Fairbanks, these fishes begin their upstream movement in late June and early July. The larger fish begin their migration first, moving upstream in a seemingly rather indefinite fashion across the Minto Flats. As the summer progresses, the fish congregate in the lower reaches of the river east of the Minto Flats. In the middle to latter part of September, there is a concentrated upstream movement of virtually the entire adult population. This is a journey of approximately 150 km to the spawning areas and is accomplished in a period of 2 to 4 wk (Kepler[1]; Townsend and Kepler[2]).

On 2 October 1975, we collected 25 (10 males, 15 females) Alaska whitefish and 23 least cisco in the Chatanika River near Fairbanks, Alaska. The fish were seined at two locations, one approximately 6.6 river km below the Elliott Highway bridge (lat. 65°4.5′N, long. 147°45.6′W), the other 3.1 km farther downstream (lat. 65°3.7′N, long. 147°47.3′W) between 1000 and 1200 h. Water depths were 0-2.5 m; water temperature was 1.5°C. These locations are within the major spawning area of the least cisco in the Chatanika River. A few Alaska whitefish also spawn in this part of the river, but their major breeding grounds lie some 15-25 km farther upstream. All the least cisco were fully ripe and running eggs or milt. The Alaska whitefish were all mature but not quite fully ripe. Most of the eggs of the females were still in fairly firm skeins. We estimated that these fish would not have spawned for another 2 wk.

The stomachs of all the fish were removed after return to the laboratory in the evening and stored in 10% Formalin[3] and the contents analyzed during the following 2 wk. Egg counts of each stomach were made by counting the eggs in each of two 1-ml samples, then estimating the total by comparison with the total volume of eggs in the stomach.

The stomachs of all least cisco were much reduced in size. Except for one containing six fish eggs and another with five unidentified seeds, all were empty. By contrast, the stomachs of all the

[1]Kepler, P. P. 1973. Population studies of northern pike and whitefish in the Minto Flats complex with emphasis on the Chatanika River. Alaska Dep. Fish Game, Fed. Aid Fish Restoration, Annu. Prog. Rep. Proj. F-9-5, Job G-II-J. 14, 23 p.

[2]Townsend, A. H., and P. P. Kepler. 1974. Population studies of northern pike and whitefish in the Minto Flats complex with emphasis on the Chatanika River. Alaska Dep. Fish Game, Fed. Aid Fish Restoration, Annu. Prog. Rep. Proj. F-9-6, Job G-II-J. 15, 21 p.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Alaska whitefish were more or less distended and crammed with eggs, almost all of them least cisco eggs. A few larger eggs in the stomachs were probably those of the Alaska whitefish.

Volume of eggs per stomach ranged between 1.5 and 42.4 ml ($\bar{x}$ = 19.96 ml). Numbers of eggs per stomach ranged between 200 and 7,842 ($\bar{x}$ = 3,574). Other items, present only in insignificant amounts, included Diptera, Tendepedidae, Trichoptera, Hydracarina, unidentified insect parts, a tree bud, and a small slimy sculpin, *Cottus cognatus*.

As indicated previously, extensive life history studies of this species conducted by the Alaska Department of Fish and Game have shown that prespawners do not feed. Presumably, then, the phenomenon reported here is of rare occurrence. However, if the entire Alaska whitefish population of the Chatanika River, estimated at 7,000 to 8,000 fish (see footnotes 1, 2) should engage in this activity, then it might constitute a major source of egg mortality for the least cisco population. Since both species are important components of the sport fishery resources of the Chatanika River, the matter is worth further investigation.

The samples reported upon here were collected as part of a study of the environmental effects of the Trans-Alaska Pipeline crossing of the Chatanika River. This study is conducted jointly by the Division of Life Sciences, University of Alaska, Fairbanks, Alaska, and the Arctic Environmental Research Laboratory, Environmental Protection Agency, Fairbanks, and is supported by the Environmental Protection Agency.

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EGG MORTALITIES IN WILD POPULATIONS OF THE DUNGENESS CRAB IN CENTRAL AND NORTHERN CALIFORNIA[1]

A recent study (Fisher and Wickham 1976) of eggs from wild populations of the Dungeness crab, *Cancer magister*, collected in the 1974-75 season showed that epibiotic fouling and egg mortalities occurred more heavily in the Drakes Bay region of central California than in the other California regions sampled (Pacifica, Point Reyes, Bodega Bay, Russian River, Gualala, Fort Bragg, and Eureka). The paper suggested that nutrients from San Francisco Bay were carried northward by the Davidson Current (the prevalent coastal current during the winter months) causing an increase in epibiotic fouling which restricted gaseous exchange across the egg membrane and increased egg mortalities.

[1]This work is a result of research sponsored by NOAA Office of Sea Grant, U.S. Department of Commerce, under Grant No. 04 5 158-20 NOAA. This work is also supported by California State Legislature Funds for Aquaculture.

In the laboratory it has been shown (Fisher 1976) that increased phosphate and nitrate levels in the seawater did, in fact, increase the number of epibiotic filaments and concurrently the number of egg mortalities. Conversely, chemotherapeutic and antibiotic treatment reduced filamentous growth and egg mortalities. It was also shown that both the number of filaments and the number of egg mortalities decreased exponentially with increasing depth into the egg masses (to a depth of 9 mm).

This study is similar to the original field study (Fisher and Wickham 1976) with modifications based on the information gained in the laboratory. All samples were collected from the same position on the egg masses to discount probable errors due to mortality variations within each egg mass. Only samples with eyespot development and no signs of hatching were used, restricting the variation in developmental states to approximately 2 wk. Mortality estimates were made from both the peripheral eggs of a sample and the total sample to determine the in situ significance of the peripheral mortalities reported for the laboratory conditions (Fisher 1976).

Procedures

The crab eggs were sampled between 26 December 1975 and 27 January 1976 from four regions: Pacifica, Drakes Bay, Russian River, and Eureka. Relative to the mouth of San Francisco Bay, Pacifica is slightly south, Drakes Bay slightly north, Russian River 80 km north, and Eureka 400 km north. Samplers in each area were supplied with curved forceps, vials partially filled with 10% Formalin[2] in seawater, and a data sheet for recording date, depth, and Loran reading for each sample collected. As ovigerous females were captured, small clusters of eggs were removed about 1-2 cm from the posterior tip of the abdomen along the midventral line with the curved forceps and placed in the vials of preservative.

After arrival at Bodega Marine Laboratory, the samples were examined under a dissecting microscope for the presence of eyespots. The samples were discarded if eyespots were lacking or if embryos were beginning to hatch. Laboratory observations have shown the time from eyespot appearance to the time of hatch to be about 2 wk while the entire external incubation period is about 2 mo.

Ten setae were randomly selected from the remaining samples (Pacifica, 27; Drakes Bay, 17; Russian River, 21; Eureka, 23). The first 25 eggs on the distal ends of these setae were examined under the dissecting microscope for mortalities. This provided a peripheral mortality estimate. Percentage peripheral mortalities were calculated from the average mortalities for each region.

The 10 setae from each sample were returned to the sample vials and transferred to a second investigator. Ten to fifteen setae were then randomly selected and an overall mortality estimate was obtained by counting all the live and dead eggs in this subsample (approximately 1,500 eggs). Percentage overall mortalities were calculated for each sample and then averaged for each region.

Results

Drakes Bay samples had the highest mortalities, while those from the Russian River and Eureka had the lowest. The peripheral and overall mortality estimates were consistent for all regions except for Drakes Bay where peripheral mortalities averaged 39.4% and overall mortalities averaged 27.6% (Table 1). A Student's t statistic for the means of two samples showed all regions except Eureka and the Russian River to be significantly different ($P<0.05$) from all other regions using both peripheral and overall mortalities. By the same analysis, the peripheral and overall mortalities within each region were statistically similar ($P>0.1$).

TABLE 1.—Average Dungeness crab egg mortalities for each region sampled. The first 25 eggs on the distal end of 10 setae from each sample were examined.

Region	No. samples	Mortalities	
		Peripheral	Overall
Pacifica	27	14.6 ± 2.0	17.4 ± 1.8
Drakes Bay	17	39.4 ± 5.4	27.6 ± 5.0
Russian River	21	8.1 ± 1.0	9.7 ± 1.4
Eureka	23	9.1 ± 1.6	11.5 ± 1.6

Discussion

These results agree with the original study completed during the 1974-75 season. High numbers of egg mortalities were found in the Drakes Bay region and low numbers in samples from the Eureka and the Russian River regions.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The lower mortalities from the adjacent Pacifica and Russian River regions confirm the suggestion of the original study that the heavy mortalities were substantially confined to the Drakes Bay region. This is consistent with the suggestion that the northerly Davidson Current may be sweeping harmful effluent from San Francisco Bay into Drakes Bay. The intermediate mortality levels of the Pacifica region could simply be a result of proximity while the Russian River region might remain relatively unaffected due to blockage and dispersion caused by the Point Reyes land mass and to dilution of the harmful effluent.

The similarity between the peripheral and overall mortalities found for the Pacifica, Russian River, and Eureka regions show a constant mortality distribution throughout the egg masses in these areas. The Drakes Bay region, however, showed considerably higher peripheral mortalities (39.4%) compared with the overall mortalities (27.6%). It is surmised that the peripheral mortalities are the primary difference between the high number of mortalities found in Drakes Bay and the lower numbers in other regions. This parallels the distribution of mortalities caused by epibiotic fouling in the laboratory (Fisher 1976) which were found to decrease with increased depth into the egg mass and further supports the proposition that epibiotic fouling contributes to egg mortalities in the Dungeness crab population of Drakes Bay.

There are several similarities between this egg disease and that of the blue crab, *Callinectes sapidus*, caused by the fungus, *Lagenidium callinectes* (Couch 1942; Sandoz et al. 1944). Both conditions are geographically selective, cause peripheral mortalities, cause greater damage on older egg masses, and coincide with increased nemertean worm populations (Rogers-Talbert 1948; Fisher and Wickham 1976). It is interesting to note that some epibiotic microorganisms were also observed on the blue crab eggs (Rogers-Talbert 1948). These similarities may indicate a common factor such as environmental stress or physiological impairment of the eggs that supercedes the importance of the respective etiological agents.

It is difficult to ascertain the effect of the Dungeness crab egg mortalities in Drakes Bay on the recruitment of the commercially important adult stages. Specific production data for Drakes Bay and migration patterns for the species are unknown. Although no attempts have been made to bear out the suggestion, Rogers-Talbert (1948) felt that 25% mortality found on the blue crab eggs could not be regarded as a factor in (adult) population fluctuations. Recently, larval stages of the Dungeness crab have also been found susceptible to epibiotic microbial infestation in the laboratory (Fisher and Nelson[3]) although no field data are available. It can at least be speculated that the combined losses of egg and larval stages have decreased the adult population of Dungeness crabs in Drakes Bay. This decrease is reflected by the collapse of the fishery in central California since 1960 while northern California production, although fluctuating, has been maintained (Orcutt et al. 1975).

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FISHERY WASTE EFFLUENTS: A SUGGESTED SYSTEM FOR DETERMINING AND CALCULATING POLLUTANT PARAMETERS

JEFF COLLINS AND RICHARD D. TENNEY[1]

ABSTRACT

An improved and simplified system to test for pollutants in shrimp waste effluents is presented. In addition, two methods were developed to calculate both protein and oil and grease content. The first method is based on establishing empirical regressions of protein or oil and grease on total residue. The second and preferred method, a simultaneous equation, is independent of these correlations but dependent on the total residue and chemical oxygen demand (COD) of the waste effluent obtained through routine analyses. The COD value was found to depend upon the amount of potassium dichromate remaining at the completion of the 2-h reflux period. The dichromate can vary from 0 to 6.25 meq excess and between 2 and 5 meq, the COD will vary 4.2%. A table of factors is given to correct the COD to 3.5 meq excess. Coefficients of COD were determined on a number of preparations of protein and oil and grease from shrimp waste effluent and from fish and shellfish. These coefficients (1.338 mg COD/mg protein and 2.678 mg COD/mg oil and grease) were required for the simultaneous equation. The simple analytical tests and mathematical treatment used in this system would be less expensive to the industry and would result in a more accurate and comprehensive evaluation of the waste load than currently obtainable by methods specified in the monitoring regulations.

An improved testing program for fishery waste effluents has been suggested (Collins and Tenney 1976) in which the total residue (TR) and the chemical oxygen demand of the filterable residue (COD_{FR}) were to be determined by analysis and used to calculate other parameters from equations previously established for a particular plant and process. It was also suggested that the protein and oil and grease (O&G) content could probably be calculated from COD and TR data to give more accurate values than by direct analyses.

The purpose of this study was to test the validity of such a testing-calculating system on waste effluents from a shrimp plant in Kodiak, Alaska. A further purpose was to derive equations whereby O&G and protein could be calculated from COD and TR data.

EXPERIMENTAL

Grab samples were taken at specific times during the shrimp production periods to obtain a range in values that would be useful for subsequent mathematical treatment. Waste effluents were taken from the underflow of a Bauer Hydrasieve[2] (1 mm, 0.04 inch) in a plant processing shrimp with combined Model A and PCA peelers. The methods of analysis and the method of calculating data are similar to those reported previously (Collins and Tenney 1976). The test for filterable residue (FR) was modified, however, to give sufficient filtrate (900 ml) for duplicate macro-Kjeldahl, COD, FR, and ash analyses. About 1,000-ml effluent, after settling 30 min, was decanted through a plug of glass wool in a powder funnel positioned over a 600-ml coarse sintered glass funnel containing GF/A glass filter paper and ¼ inch of dry base-acid-water washed ASTM standard Ottawa sand (C-190). The suction flask was evacuated briefly several times during filtration and clamped off to prevent plugging of the filter and evaporation. We have found that use of continuous evacuation causes rapid plugging of the glass filter paper and, additionally, could cause considerable errors through evaporation.

As will be discussed later, the precision of the residue and ash analyses is particularly important. Consequently, considerable attention was given these analyses to obtain good precision as well as convenience in conducting the analyses. The major steps of the procedure follow:

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[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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1. Heat 100-ml Pyrex beakers at 500°C for 1 h, air cool for 1 h, and weigh. Prior to use, new beakers should be equilibrated to ashing conditions.
2. Accurately weigh about an 80-ml sample of effluent into the dry beaker. Dry overnight at 103°C in a forced draft oven and weigh after 1 h of air cooling.
3. Calculate TR in milligrams/liter. (Note: this system, of course, gives TR in milligrams/1,000 g, but we follow the convention and express it in milligrams/liter.)
4. Heat beaker and dried sample at 500°C for 2 h, air cool 1 h, and weigh as before.
5. Calculate ash from the initial weight of sample, express as milligrams/liter as in step 3.

RESULTS

In general, these effluent samples were tested for COD, residue, ash, O&G, and protein. The data in Table 1 are averages of duplicate analyses, except O&G which is in triplicate. The data should not be considered representative of the effluent from this plant because of the specific way of taking these grab samples. Comparisons in relative data, however, can be made. For example, the COD of the filterable residue (COD_{FR}) was slightly over one-half of the total COD (COD_{TR}) and the filterable residue (FR) was 64% of the total residue (TR) on an ash-free basis. The TR contained 17% ash, but most of the ash was found in the FR fraction (92%) leaving only 8% in the nonfilterable residue (NFR) fraction.

The relationship between COD and ash-free residue is plotted in Figure 1 and that for O&G and protein versus ash-free residue is given in Figure 2. The coefficients of correlation were 0.99 and 0.97 for the COD regressions on TR_K and FR_K, respectively. The *F*-test for linearity at the 95% level of significance was 0.015 for the TR_K line and

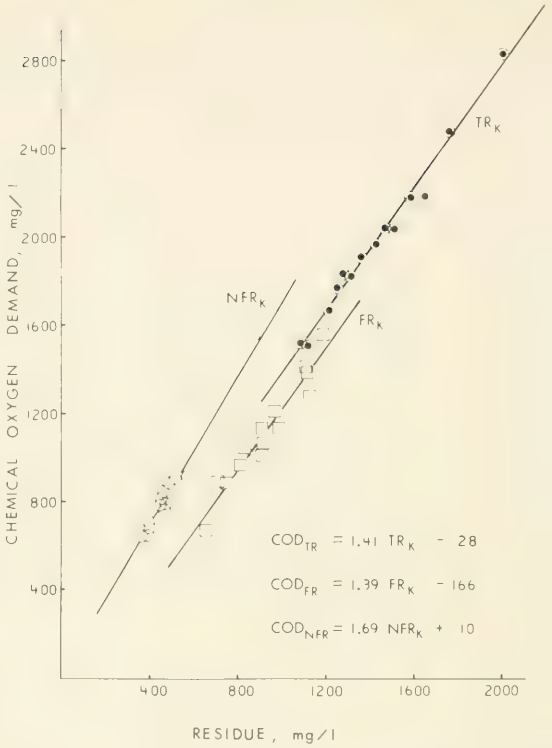

FIGURE 1.—Relationship between the COD and the concentration of the ash-free residue in waste effluents from a plant using both Model A and PCA peelers and fresh water.

TABLE 1.—Analyses of screened shrimp waste effluents from a plant using both Model A and PCA mechanical peelers. [All values in milligrams/liter.]

Sample number	Chemical oxygen demand		Residue		Ash		Protein (6.25N)		Oil and grease
	TR	FR	TR	FR	TR	FR	TR	FR	TR
1	1,517	672	1,420	946	304	291	831	522	185
2	2,839	1,280	2,328	1,441	325	310	1,319	859	486
3	2,190	1,016	1,911	1,146	264	241	1,215	785	276
4	2,182	1,413	1,897	1,400	308	288	1,281	947	258
5	1,824	1,139	1,567	1,146	261	242	1,056	790	203
6	1,917	1,210	1,602	1,182	242	220	1,075	806	230
7	2,039	1,393	1,833	1,418	324	298	1,212	944	229
8	1,771	964	1,532	1,061	280	256	1,037	744	195
9	2,481	1,565	2,137	1,522	378	332	1,425	1,072	302
10	1,969	1,066	1,750	1,197	321	284	1,175	835	204
11	1,666	883	1,460	965	247	224	1,025	703	186
12	1,829	1,046	1,573	1,093	286	263	1,116	794	175
13	2,041	1,156	1,822	1,310	352	328	1,188	863	233
14	1,522	883	1,351	946	256	228	925	644	148
Mean	1,985	1,120	1,727	1,198	296	272	1,134	808	236
SD	361	240	280	193	41	38	158	136	83

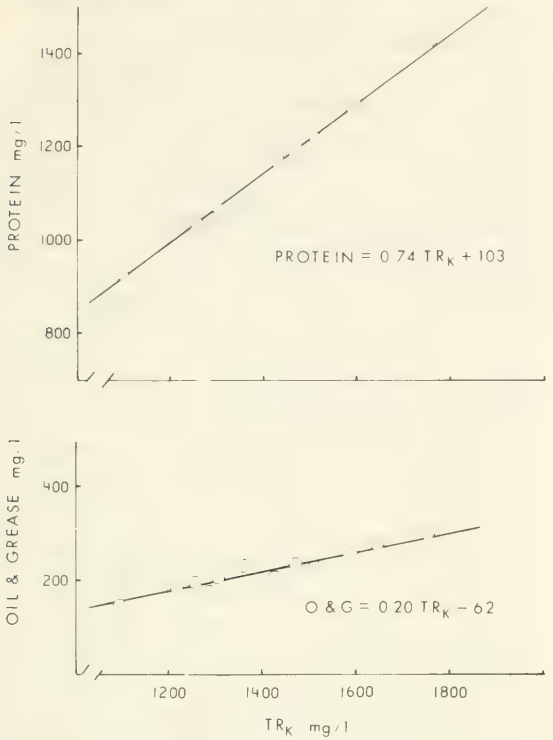

FIGURE 2.—Relationship between the concentration of protein or oil and grease and the concentration of the ash-free total residue in waste effluents from a plant using both Model A and PCA peelers and fresh water.

0.068 for FR_K. The regression lines and equations found in Figures 1 and 2 include a correction for ash content in the residue, i.e., TR − ash = TR_K. These equations, obtained by the method of least squares, are as follows:

$$COD_{TR} = 1.41\ TR_K - 28 \quad (1)$$
$$COD_{FR} = 1.39\ FR_K - 166 \quad (2)$$
$$COD_{NFR} = 1.69\ NFR_K + 10 \quad (3)$$
$$\text{Protein} = 0.74\ TR_K + 103 \quad (4)$$
$$O\&G = 0.20\ TR_K - 62 \quad (5)$$

In our previous paper we suggested that background data for a particular plant should be determined [Equations (1), (2), and (3)] so that the other parameters could be calculated from routine tests for TR and COD_{FR}. Since usage of salt and seawater in plants tends to vary, we now also suggest that an ash analysis be done to eliminate variability in the total residue. Once background data have been established for a particular plant or product process, our testing-calculating system would proceed as follows: Determine TR and ash and substitute the difference into Equation (1) and solve for COD_{TR}. Using the mean values for TR and ash of Table 1 gives 1,431 mg/liter TR_K. Substitution into Equation (1) gives 1,990 mg COD_{TR}/liter which nearly agrees with the mean analytical COD value. Similarly, the other recommended routine test for COD of the filtrate (COD_{FR}) gives a mean value from Table 1 of 1,120 mg/liter which, when substituted into Equation (2), gives 925 mg/liter for FR_K, in agreement with the difference between FR and ash, i.e., FR − ash = 926 mg/liter. The NFR or COD_{NFR} are obtained by difference, e.g., $TR_K - FR_K = NFR_K$. In order to calculate protein and O&G, the TR_K can be substituted into Equations (4) and (5). A rough estimate of O&G content can also be obtained by dividing the COD by 9 which is the average for the ratio of COD to the weight of O&G. The ratio actually varies from about 8 to 10 and inversely with the COD. The ratio and equations only have application to this plant and processing conditions. For other processing conditions or plants, the baseline data and equations should be determined in the same manner.

CALCULATION OF O&G AND PROTEIN USING A SIMULTANEOUS EQUATION

In this section we will derive a simultaneous equation that can be used as a substitute for direct analysis so that O&G and protein can be calculated by using routine data on COD_{FR}, TR, and ash. The equation is based on the assumption that the sum of the COD of each component in the effluent equals the total COD, i.e., COD $(x_1 + x_2 \ldots x_n)$ = total COD; and that the sum of the weights of each constituent having an effect on COD equals the total residue minus ash, i.e., Residue $(x_1 + x_2 \ldots x_n)$ = Total residue − ash.

To develop the simultaneous equation, coefficients must first be determined that relate COD to the two major constituents of a fishery waste (protein and O&G). In addition, the residue-ash relation needs defining.

COD in Relation to Protein and O&G

To establish a relationship between COD and pollutants, we prepared samples of protein and

O&G and determined their COD equivalent by direct analysis.

To prepare protein a sample of muscle was washed with water and centrifuged to remove the blood and other small nitrogen components, then washed with 2-propanol (IPA) to remove part of the water. The sample was blended and refluxed twice with IPA followed by filtration, washing, and refluxing with petroleum ether (PE) and overnight drying at 103°C. These oil free, white, odorless protein samples were analyzed for nitrogen by the standard macro-Kjeldahl method (Horwitz 1965:273) and for COD. The COD factor was calculated on a 100% protein basis.

To obtain O&G, the sample of fish or shellfish was briefly rinsed with water and IPA; then, using a high speed blender and anhydrous conditions ($MgSO_4$), the O&G was extracted, cold, with IPA and PE. For waste effluent, O&G was obtained by the analytical method used previously (Collins 1976). By either method, after weighing the dry O&G and diluting to volume with PE an aliquot of the final solution equivalent to 8-10 mg O&G was evaporated in the COD flask, oven-dried for 0.5 h, and used for COD determination. Since PE has a residue significantly affecting COD, freshly distilled PE was used throughout the tests.

The COD equivalent was determined on a number of different preparations of O&G and protein from fish and shellfish muscle and from shrimp waste effluent. The average values of from 5 to 30 replicate COD analyses for each material are given in Table 2.

The COD coefficients for protein are in reasonable agreement and are probably independent of species or product form. The theoretical COD coefficient of protein was calculated using amino acid percentage composition data for snow crab reported by Krzeczkowski and Stone (1974). The theoretical figure of 1.285 mg COD/mg protein was in close agreement with our experimental figure of 1.338. The coefficients for O&G, however, are quite different and are presumably caused by errors in the COD method, differences in species, product, and perhaps slight differences in the method of extracting. There are, of course, known differences in the lipid composition of these species, especially the C-20 and C-22 polyunsaturated fatty acids. The chain length and configuration of the lipids would have a positive effect on the COD coefficient. For example, some theoretical coefficients are: acetic acid (C_2) 1.066, propionic (C_3) 1.514, myristic (C_{14}) 2.807, melissic (C_{30}) 3.115, lecithin ($C_{44}H_{88}O_9NP$) 2.458, and tristearin ($C_{57}H_{110}O_6$) 2.934. Recognizing the wide variations possible, the empirically derived coefficient of 2.678 seems reasonable.

TABLE 2.—The COD coefficient of several preparations of oil and grease (O&G) and protein from fish and shellfish and from shrimp waste effluent.

Starting material	COD of 1.0 mg/liter of O&G	COD of 1.0 mg/liter of Protein
Black cod, frozen		1.328
Pollock, frozen		1.328
Snow crab, frozen	2.631	
Pink salmon, fresh	2.795	1.326
	2.818	1.345
Pink shrimp, fresh	2.710	1.349
	2.505	1.270
		1.328
Pink shrimp, canned	2.757	1.414
	2.584	1.350
	2.518	
	2.736	
Shrimp waste effluent	2.788	
	2.618	
Mean	2.678	1.338
SD	0.112	0.037

These coefficients are used along with the concentration of protein and O&G to give the COD, i.e., (1.338 mg COD/mg protein)mg protein + (2.678 mg COD/mg O&G)mg O&G = COD_{TR} and assumes that the total COD is the sum of the COD of these two major constituents. To check the validity of this equation the coefficients were multiplied by the predicted values for protein and O&G [obtained from TR_K data and Equations (4) and (5)] and the resulting mean of the sums of the products (2,155 mg COD/liter) was found to be 1.083 times greater than the mean predicted value for COD_{TR} (1,990 mg COD/liter) obtained from TR_K data and Equation (1). Although difficult to prove or demonstrate, we believe that the lower analytical values for COD in a sample of waste effluent are caused by the unequal and competing oxidation of protein and O&G. As is well known, O&G reacts slowly and especially if the dichromate concentration has been reduced from reacting with the more easily oxidized protein. Minor constituents such as nonprotein nitrogen and carbohydrates would contribute to COD in a ratio different from the protein coefficient.Regardless, if the simultaneous equation is to be developed, the inequality must be adjusted by increasing the COD value to equal the sum of the COD of protein plus O&G, i.e.,

$$1.338 \text{ protein} + 2.678 \text{ O\&G} = 1.083 \text{ COD}_{TR}. \quad (6)$$

COD Reaction

The oxidation reaction in the COD method follows the usual chemical reaction laws, i.e., the completeness of the reaction is dependent upon the concentration of the reactants (potassium dichromate and waste). The method uses 25 ml 0.25N or 6.25 meq $K_2Cr_2O_7$ in the reaction flask and 50 ml of effluent. If the effluent is relatively strong, most of the dichromate will be expended in the reaction which results in an incomplete reaction and a lower COD value than if the waste were weak, i.e., having a larger excess of dichromate at the completion of the reaction. Moore and Walker (1956) recommended that the size of sample should be selected so that not more than 50% of the potassium dichromate is used up during the oxidation. To illustrate the relationship between COD and amount of dichromate remaining (the excess) at the end of the 2-h reflux period, data from six protein preparations were combined and plotted in Figure 3. The equation of the regression line was then used to calculate correction factors so that if the COD were determined at an excess dichromate level above or below an arbitrary point of 3.5 meq, the value can be corrected to its value at 3.5 meq. These correction factors are listed in Table 3. To correct COD values, determine the excess dichromate (titration value times normality) and multiply the corresponding factor from Table 2 by the COD determined in the usual way.

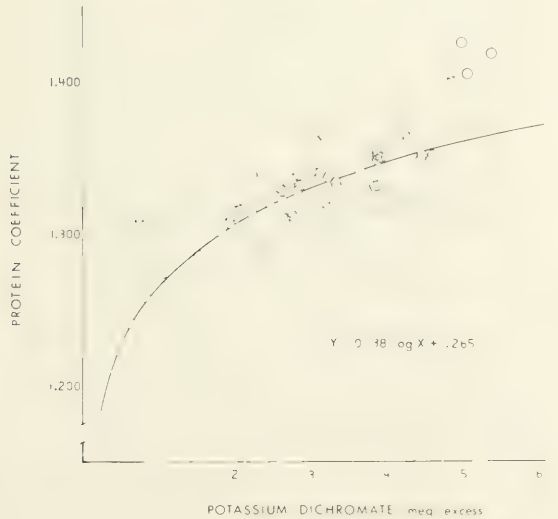

FIGURE 3.—Relationhship between the protein coefficient and the amount of dichromate remaining at the end of the 2-h reflux period.

TABLE 3.—Multiplication factors to correct COD to 3.5 meq dichromate excess.

Excess dichromate (meq)	Multiplication factor	Excess dichromate (meq)	Multiplication factor
2.0	1.026	3.6	0.999
2.1	1.024	3.7	0.998
2.2	1.021	3.8	0.996
2.3	1.019	3.9	0.995
2.4	1.017	4.0	0.994
2.5	1.015	4.1	0.993
2.6	1.014	4.2	0.992
2.7	1.012	4.3	0.991
2.8	1.010	4.4	0.990
2.9	1.009	4.5	0.989
3.0	1.007	4.6	0.988
3.1	1.005	4.7	0.987
3.2	1.004	4.8	0.986
3.3	1.002	4.9	0.985
3.4	1.001	5.0	0.984
3.5	1.000		

Since titration (Jirka and Carter 1975), sample, or reaction errors occur at either end of the curve, we suggest that COD values are valid only between 2 and 5 meq excess. All data for the protein coefficients were determined by obtaining from 10 to 30 COD values at different addition levels (5 to 30 mg protein/50 ml) and plotting the regression line. The coefficient was obtained by substituting the logarithm of 3.5 meq excess into the equation for the regression and solving for COD. In addition, all COD data in Table 1 were corrected to 3.5 meq excess dichromate.

Residue-Ash Correction

The major components of the total residue that contribute to COD are protein and O&G. In addition, various salts and dirt contribute to TR and possibly to COD. Unfortunately, there is no convenient method to measure these minor constituents so we estimate them by determining ash and then subtract to give a corrected value for TR. Since the weight of ash obtained after 500°C drying is less than its corresponding weight when dried at 103°C, the TR_K value (TR − ash) is accordingly greater than it should be. Therefore, the TR_K was reduced as follows: To eliminate variability in individual values, the O&G and protein values were predicted using Equations (4) and (5) for the regression lines in Figure 2 and TR_K data. The sum of the weight of protein plus O&G was found to be about 3% smaller than TR_K, i.e.,

$$\text{protein} + \text{O\&G} = 0.969\ TR_K. \quad (7)$$

This equation corrects the TR_K so that it equals the sum of the protein and O&G, and is convenient to use in this form in the simultaneous equation. The constant, 0.969, is the result of increasing the analytical value for ash by 15.2% and represents, in part, the difference in weight of ash between drying at 500°C and 103°C.

Simultaneous Equation

In the preceding discussion we have shown the two parts of the simultaneous equation: the first showing the sum of the COD from protein and from O&G to be equal to an adjusted total COD, and the second showing the sum of the weights of protein and O&G to be equal to the total residue minus the ash content and corrected for the difference in weight caused by drying at 500°C or 103°C. Equations (6) and (7) are combined in the following so that a simple calculation can serve as a substitute for the difficult direct analyses for protein and O&G:

$$\begin{aligned} X + Y &= 0.969\ TR_K \\ 1.338X + 2.678Y &= 1.083\ COD_{TR} \end{aligned} \quad (8)$$

where: X = protein in milligrams/liter
Y = O&G in milligrams/liter.

This equation should have general application to fishery waste effluents provided: 1) TR_K and COD_{TR} are known or can be derived, and 2) the constant used to increase the value for COD_{TR} has general application. If our assumption is correct that the COD is low because of the incomplete and competitive oxidation of protein and O&G, the constant would apply to any fishery waste having a similar relative amount of protein and O&G, i.e., about 5:1, respectively.

The mean TR and ash data from Table 1 are used to illustrate the use of this equation: From Table 1, TR − ash = 1,431 mg/liter and when substituted into Equation (1) gives a value of 1,990 mg/liter for COD_{TR}. These values, when substituted into the equation and solved for X and Y, give,

$$\begin{aligned} X + Y &= 0.969(1{,}431) \\ 1.338X + 2.678Y &= 1.083(1{,}990) \end{aligned}$$

where: X = 1,163 mg protein/liter
Y = 224 mg O&G/liter.

The calculated values are 29 mg higher for protein and 12 mg lower for oil than the mean analytical values of Table 1 (1,134 and 236, respectively). The differences between data obtained by the direct analysis for protein and O&G and the two methods of calculation are compared in Table 4. A negative or positive sign indicates whether the calculated value is less or more than the analytical value.

The analytical values of sample numbers 1, 2, 3, and 12 for protein and 2 for O&G are obviously in error and although these values were included in the mean values in Table 1, they were omitted from the regression lines and equations of Figure 2. The comparative data indicate that the calculated values are in reasonable agreement with analytical values. Since a regression line determined by the method of least squares is by definition the best fit of empirical data containing normal errors in precision and accuracy, and since protein and O&G are less accurate analyses than TR_K or COD, it follows that a value for O&G calculated from the simultaneous equation or from the equation of the regression line should be more correct than an individually determined value. The data of Equations (4) and (5) in Table 4 are merely a measure of the fit of each value to the regression line. The data of Equation (8), however, are independent of protein and O&G but dependent upon COD and TR data.

If the simultaneous equation is used to calculate O&G, TR_K and COD_{TR} are required for the equation and can be obtained through analysis and calculation, respectively. Alternatively, O&G or

TABLE 4.—Comparison by difference of protein and O&G data obtained by analysis or by calculation.

Sample no.	Protein mg/liter			O&G mg/liter		
	Analysis	Eq. (4)	Eq. (8)	Analysis	Eq. (5)	Eq. (8)
1	831	+98	+104	185	−24	−39
2	1,319	+266	+265	486	−147	−129
3	1,215	+107	+206	276	−9	−101
4	1,281	−2	+33	258	−2	−32
5	1,056	+13	−1	203	−4	+8
6	1,075	+34	+9	230	−20	+4
7	1,212	+8	+63	229	+11	−42
8	1,037	−8	−44	195	−7	+25
9	1,425	−20	−24	302	−12	+2
10	1,175	−15	+1	204	+20	+5
11	1,025	−24	−22	186	−5	−13
12	1,116	−61	−102	175	+20	+59
13	1,188	+3	+9	233	−1	−6
14	925	−12	−35	148	+9	+23

protein can be calculated from the regression of O&G and protein on TR_K. For practical reasons, we prefer using the simultaneous equation because establishing the base data would be difficult at the plant level in that both protein and O&G should be determined and correlated with COD and TR_K to establish the accuracy of the analyst.

Occasionally, wild values might occur in analyses but the average of the standard deviations between duplicate analyses for TR_K, FR_K, COD_{TR}, and COD_{FR} in this paper was 6.1, 3.6, 14.4, and 10.1 mg/liter, respectively. Using the 6 mg/liter TR_K figure the predicted value for COD from 1,431 ± 12 mg TR_K is 1,990 ± 17 mg COD from Equation (1). Based on this interval of two standard deviations, protein and O&G values obtained by the simultaneous equation could vary as follows:

TR_K	COD_{TR}	Protein	O&G
1,419	1,973	1,153	222
1,431	1,990	1,163	224
1,443	2,007	1,172	226

RECOMMENDATION

We recommend that this simplified testing-calculating system be used by the fishing industry provided proper regulatory approval is obtained. The following background data will be required:

1. Determine the regression of COD_{TR} and COD_{FR} on TR_K and FR_K and calculate the equations [i.e., Equations (1), (2), (3)]. Use grab samples (about 10) to give a good spread of data.
2. For protein and O&G, either a regression or a simultaneous equation can be used.
   (A) Obtain O&G and protein data on the same samples as above and determine the equation of the regressions of protein and O&G on TR_K [i.e., Equations (4) and (5)].
   (B) Determine the ratio or weight of protein to weight of O&G on several samples and if between 4.6 and 5.9, the constant (1.083) in Equation (8) is assumed valid. If not, the constant must be recalculated in order that the COD_{TR} equals the sum of COD from protein and O&G [see discussion for Equation (6)].
   (C) The O&G coefficient should be determined on fishery waste effluents in which the oil may give a significantly different value than 2.678.

The routine application of this system would be as follows:

1. Determine COD_{FR}, TR, and ash by direct analysis.
2. Subtract ash from TR to give TR_K.
3. Substitute into Equations (1) and (2) and solve for COD_{TR} and FR_K.
4. Obtain COD_{NFR} and NFR_K by difference or by Equation (3).
5. Obtain protein and O&G from Equations (4), (5), or (8).

Thus, three simple and accurate tests give reportable data on nine parameters which more completely describe the pollutant load released to the environment than those currently in use.

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AMERICAN SOLENOCERID SHRIMPS OF THE GENERA *HYMENOPENAEUS, HALIPOROIDES, PLEOTICUS, HADROPENAEUS* NEW GENUS, AND *MESOPENAEUS* NEW GENUS

ISABEL PÉREZ FARFANTE[1]

ABSTRACT

Twelve American species, one from Hawaii, are assigned to five genera: five to *Hymenopenaeus,* one to *Haliporoides,* two to *Pleoticus,* three to *Hadropenaeus,* and one to *Mesopenaeus;* the latter two genera are described herein. Each of the genera is defined and the relationships among them are discussed. The species are described in detail mostly on the bases of collections made in the western Atlantic and eastern Pacific during cruises of 29 exploratory vessels. For each species a diagnosis, illustrations, references, disposition of types, locality records, and geographic as well as bathymetric ranges are provided. The affinities of each species are indicated, and variations of several morphological and morphometric characters are analyzed. Keys for the identification of all taxa are given. Photophores were discovered in *Hadropenaeus affinis,* here recognized as a distinct species, and *Mesopenaeus tropicalis.* The spermatophores of three, *Pleoticus robustus, P. muelleri,* and *M. tropicalis* (those of the latter previously unknown), are described and their mode of attachment to the females is discussed. The range of *Hymenopenaeus debilis* was found to extend south of the Gulf of Mexico, through the Caribbean to Guyana, and that of *H. aphoticus* to include the Caribbean. *Pleoticus muelleri* is now known to occur north of the state of Rio de Janeiro, off Espírito Santo, and *Hadropenaeus affinis* is newly reported from the southeast Atlantic coast of the United States, where it ranges as far north as Cape Lookout, N.C.

This work is part of a continuing study of the systematics and distribution of the American members of the superfamily Penaeoidea. Extensive collections made during cruises of 26 exploratory vessels provided excellent series of specimens from the western Atlantic. In contrast, the material available from the tropical and subtropical eastern Pacific (including that obtained during cruises of three exploratory vessels) is rather meager and these waters still remain appallingly unexplored, particularly beyond the 100-m contour. Few benthic collections from the latter region have been deposited in American institutions since the expeditions of the *Albatross* in 1889 and 1891. The only major ones are those resulting from the explorations sponsored by the Allan Hancock Foundation and Scripps Institution of Oceanography among which no member of the genera investigated in the present project has been found.

The only species treated here from waters not adjacent to the American continent is one which ranges throughout the Indo-West Pacific, reaching Hawaii. This shrimp is included because it is the third member of a new genus, the other two being found off American shores. Inasmuch as the Hawaiian population of the species has not been adequately described and because numerous specimens from the area are available to me, a detailed account of its morphology is presented.

The five genera treated in this paper, together with *Solenocera* and *Haliporus,* constitute the family Solenoceridae, a group that has been previously considered one of the four subfamilies of Penaeidae. I am of the opinion that because of the basic differences among these four suprageneric groups they should be elevated to the category of families, i.e., Aristeidae, Solenoceridae, Penaeidae, and Sicyoniidae, as has been defended by Pérez Farfante (in press). The western Atlantic species of *Solenocera* (the other genus of Solenoceridae which is present in the region, in addition to four of those discussed here) were recently monographed by Pérez Farfante and Bullis (1973).

In the diagnoses of the genera and descriptions of the 12 species discussed here, many morphological characters have been studied in order to base relationships at generic and specific levels.

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For each taxon a synonymy, bibliographic references (selected for the genera, and complete for the species), location of type-specimens, descriptions, and distributional data are given, as are variations for some species. Detailed accounts of the spermatophores (both as attached to the females and as they appear when removed from the terminal ampullae of the males) of three species are also presented. These are the only species for which spermatophore-bearing females were secured.

Bate (1881) was the first to describe species of the generic complex treated here, assigning all except one—which was assigned to *Solenocera* Lucas (1849)—in a new genus, *Haliporus*. A year later, Smith (1882) proposed the genus *Hymenopenaeus* for another new species belonging to that complex. Subsequently, Bate (1888) expanded his preliminary descriptions of *Haliporus* and corresponding species, and pointed out that the one he had placed in *Solenocera,* together with two others, should be relegated to a new genus, *Philonicus*. After his manuscript was in press, he discovered that the latter name was preoccupied and changed it to *Pleoticus* in the Introduction. Bouvier (1906b) presented a revision of the genus *Haliporus* in which he recognized 19 species, most of which had been described after Bate's last contribution (1888). He separated them into three groups on the basis of the relative length of the posterior two pairs of pereopods, the relative diameter of the proximal part of the respective carpi, and the consistency of the integument. He failed to recognize other important supraspecific differences which led him to group together species which are not closely related. Burkenroad (1936) disagreed with Bouvier's arrangement and, as a result of an extensive investigation, recognized two genera, *Haliporus* and *Hymenopenaeus*. Several other generic names have been proposed and later synonymized with *Hymenopenaeus,* a clear indication of the taxonomic difficulties presented by this complex.

The genus *Hymenopenaeus* was defined by Burkenroad (1936) as those "Solenocerinae without podobranchs behind VIII; with well-developed prosartema and only a single pair of lateral telson spines in adult stages, and with cylindrical filiform antennular flagella." Within it, he recognized four separate groups based on the presence or absence of branchiostegal or pterygostomian spines and the arrangement of the epigastric and rostral teeth.

An examination of Atlantic, eastern Pacific, and Hawaiian species, supplemented by material from the Indo-West Pacific region, convinces me that, in addition to the arrangement of the mid-dorsal teeth on the carapace, the following characters are more reliable than the branchiostegal and pterygostomian spines in ascertaining interrelationships of the species previously included in *Hymenopenaeus:* shape of the antennular flagella and rostrum, proportions of the carapace, number and comparative size of the articles of the mandibular palp, presence or absence of certain carinae on the carapace, relative dimensions of the posterior two pairs of pereopods, location of the distolateral spine (terminal or subterminal) of the lateral ramus of the uropod, structure of the petasma, and degree of development of the arthrobranchia on somite VII.

A comparative study based on the characters cited above indicates that the species under consideration should be assigned to five genera: *Hymenopenaeus, Pleoticus,* and *Haliporoides*—which had been erected previously—and *Hadropenaeus* and *Mesopenaeus*—which are proposed here.

Diagnoses of the four groups established by Burkenroad (1936) within *Hymenopenaeus* together with the conclusions resulting from my revision of this species-complex follow.

Group I. This division contained the western Atlantic *H. muelleri* and *H. tropicalis,* and the Indo-West Pacific (Red Sea) *H. steindachneri*. As pointed out by Burkenroad, these species share the arrangement of the epigastric and rostral teeth, which are separated by regularly decreasing intervals anteriorly, and the absence of branchiostegal and pterygostomian spines; to these characters may be added the presence of orbital spines and the lack of distinct branchiocardiac carinae. Several different features occur in *tropicalis* which I consider to be of sufficient importance to justify a separate genus, for which I propose the name *Mesopenaeus*. Moreover, the western Atlantic *robustus,* which was placed in Group II by Burkenroad, shares basic characters with *muelleri* and *steindachneri;* consequently, the three are grouped herein under the available generic name *Pleoticus* Bate (1888).

Group II. The species assigned to this group were characterized by possessing branchiostegal but lacking pterygostomian spines and, like those of Group I, exhibit epigastric and rostral teeth separated by regularly decreasing intervals.

Burkenroad subdivided the group into two sections: section 1, with orbital spines, to which only *H. robustus* was assigned, and section 2, without orbital spines, to which the western Atlantic *H. modestus* and the Indo-West Pacific *H. lucasii* were referred. As stated above, the former species is here transferred to the genus *Pleoticus,* and the latter two, together with the amphi-Atlantic *H. affinis* (which Burkenroad considered as "very doubtfully distinct" from *H. modestus*), are placed in the genus *Hadropenaeus.*

Group III. This group comprised the species with pterygostomian but lacking branchiostegal spines, and with the epigastric tooth separated from the rostral teeth by a long interval. The eastern Pacific *H. diomedeae* and the Indo-West Pacific *H. sibogae* and *H. triarthrus* were included, but these three species are referred here to the genus *Haliporoides* Stebbing 1914.

Group IV. This assemblage contained those species that are armed with branchiostegal spines, and have the epigastric and first rostral teeth separated from the remaining rostral teeth by a conspicuous interval. It was subdivided into two sections characterized by the presence or absence of pterygostomian spines. In section 1, Burkenroad cited *Hymenopenaeus laevis,* found on both sides of the Atlantic and in the Indo-West Pacific, and *H. doris* and *H. nereus* of the American Pacific; in section 2, he included the Atlantic *H. aphoticus* and *H. debilis* and the Indo-West Pacific *H. aequalis, H. obliquirostris, H. neptunus,* and *H. propinquus.* Since the publication of Burkenroad's work, one species, the Indo-West Pacific *H. sewelli,* has been added to section 1, and three have been added to section 2: one from the eastern Atlantic, *H. chacei,* and two from the Indo-West Pacific, *H. fattahi,* and *H. halli.* These species are included in *Hymenopenaeus* as restricted here, and their separation into two sections is recognized.

Burkenroad also discussed under *Hymenopenaeus* the two following Indo-West Pacific species: *Haliporus villosus* Alcock and Anderson 1894 (syntype illustrated in Alcock and Anderson 1896), and *Haliporus taprobanensis* Alcock and Anderson 1899 (holotype illustrated in Alcock 1899b). He indicated that the former perhaps would merit being placed in an independent group, and pointed out that although the latter shares several characters with members of Group III, it differs from them in other basic features. Our knowledge of *H. villosus* prior to Kensley's (1968) study was limited to the brief description by Alcock and Anderson (1894) and their illustration published in 1896 (plate 26, figure 1). The lack of detail in the figure of the telson, exhibiting no movable spines, was probably responsible for Burkenroad's assigning this shrimp to the genus *Hymenopenaeus.* Kensley presented a detailed description and several illustrations which demonstrate that this species exhibits two basic features characteristic of the genus *Haliporus* (as restricted by Burkenroad 1936): in addition to the podobranchia on the second maxilliped, another, small one is present on the third maxilliped, and the telson is armed with movable spines situated anterior to the fixed pair. My examination of two specimens of *H. taprobanensis* has shown that the same characters are present in them; thus, in respect to these two features, both this species and *H. villosus* are more closely allied to the members of *Haliporus* than to those assigned to *Hymenopenaeus.* It should be pointed out, however, that *H. villosus* and *H. taprobanensis* differ from *Haliporus curvirostris* Bate 1881, the type-species, in several characters (e.g., shape of rostrum, number of podobranchiae posterior to the second maxilliped, carinae present on the carapace) which seem to me to be of supraspecific significance. Consequently, I believe that a study of adequate material might demonstrate that they should be relegated to separate monotypic genera.

Although the illustration of the entire animal of *H. villosus* by Alcock and Anderson (1896) and that by Kensley (1968) leave little doubt that both correspond to the same species, the specimens available to the former authors were densely covered by setae, as they explicitly stated, whereas that studied by Kensley as well as the specimens examined by me are glabrous. The material available to Alcock and Anderson was from the Laccadive Sea, off southwest India; Kensley's specimen was caught off southwest of South Africa, and the two at my disposal were collected off eastern Madagascar.

All five genera (together with *Haliporus* and *Solenocera*) are believed to have arisen from a common solenoceroid ancestor, some of the characters of which are presented in the accompanying dendrogram. In the latter only the newly acquired characters or those modified or lost in each lineage are indicated. As shown in the dendrogram, one of the lines arising from the solenoceroid ancestor led to *Haliporus,* apparently not only the most primitive solenocerid, but

CHARACTERISTICS INVOLVED IN THE EVOLUTION OF SOLENOCERIDAE
(See text for explanation)

according to Burkenroad (1963b) "the Recent Peneid which seems in several respects the nearest of these to the stem-form of the relatively primitive suborder Dendrobranchiata." A second line gave rise to *Hymenopenaeus* and *Haliporoides,* and a third lineage is believed to have been ancestral to two stocks, one of which terminated in *Pleoticus* and from the other evolved *Hadropenaeus, Mesopenaeus,* and *Solenocera;* the latter appears to be the most specialized of all seven genera.

The members of Solenoceridae, in general, occupy deep water beyond the continental and insular shelves; however, most of the species of *Solenocera* as well as *Pleoticus muelleri* are restricted to shallow water. *Mesopenaeus tropicalis*

is found both on the shelves, at a minimum depth of 30 m, and on the slopes to about 500 m.

Material

Abbreviations of the repositories of the specimens examined during this study follow:

AMNH	American Museum of Natural History, New York, N.Y.
BMNH	British Museum (Natural History), London.
IOUSP	Instituto Oceanográfico, Universidad de São Paulo, São Paulo.
MCIP	Ministerio de Comercio e Industrias, Panama.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
MP	Muséum National d'Histoire Naturelle, Paris.
RMNH	Rijksmuseum van Natuurlijke Histoire, Leiden, Netherlands.
TAMU	Texas A&M University, College Station, Tex.
UMML	Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Fla.
UNC-IMS	University of North Carolina - Institute of Marine Sciences, Morehead City, N.C.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
YPM	Peabody Museum of Natural History, Yale University, New Haven, Conn.

Presentation of Data

The measurement of carapace length (cl) is the linear distance between the orbital margin and the midposterior margin of the carapace, and that of total length (tl) is the distance between the apex of the rostrum and the posterior end of the telson. The scales accompanying the illustrations are in millimeters. Figures 1 and 2 depict many characters used in the descriptions. For the terminology employed in the accounts of the spermatophores, see Pérez Farfante (1975).

Key to Genera of Solenoceridae

1. Telson with pairs of movable lateral spines anterior to fixed pair; podobranchia on at least second and third maxillipeds ..... *Haliporus*
   Telson with single pair of fixed lateral spines only; podobranchia restricted to second maxilliped 2

2. Dorsal and ventral antennular flagella lamellate; lateral ramus of uropod lacking distolateral spine ..... *Solenocera*
   Dorsal antennular flagellum subcylindrical, ventral subcylindrical or flattened; lateral ramus of uropod armed with distolateral spine 3

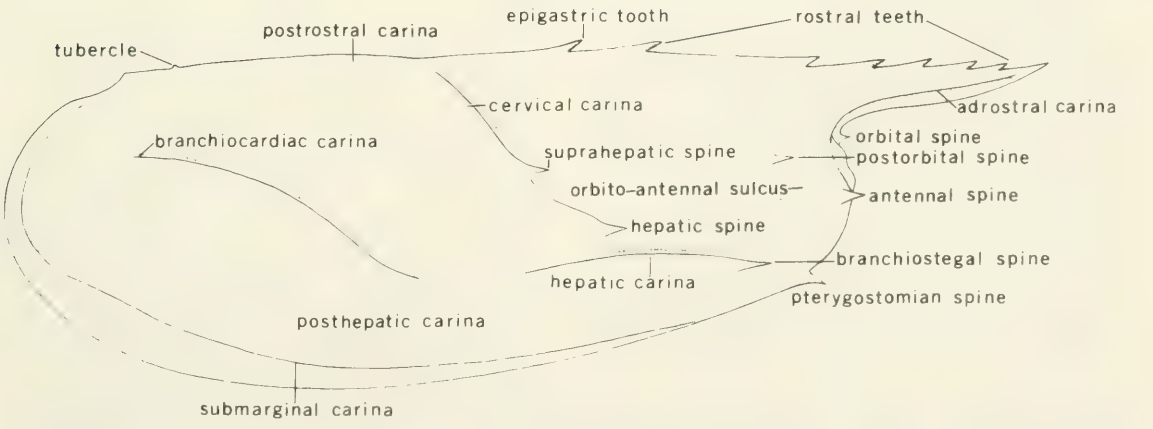

FIGURE 1.—Diagrammatic lateral view of cephalothorax showing terms used in descriptions of solenocerid shrimps.

3. Ventral antennular flagellum conspicuously depressed, orbital spine present ..... *Mesopenaeus*
   Ventral antennular flagellum subcylindrical, occasionally depressed, if so orbital spine lacking 4

4. Epigastric tooth separated from first rostral by interval not conspicuously smaller or greater than that between first and second rostral teeth 5
   Epigastric or epigastric and first rostral teeth separated from remaining teeth by relatively long interval 6

5. Rostrum low, with ventral margin straight or concave; submarginal carina present ..... *Pleoticus*
   Rostrum deep, with ventral margin pronouncedly convex; submarginal carina absent ..... *Hadropenaeus*

6. Epigastric and first rostral teeth separated from remaining ones by long interval; suprahepatic spine absent .... *Hymenopenaeus*
   Epigastric tooth separated from rostral teeth by long interval; suprahepatic spine present ..... *Haliporoides*

Hymenopenaeus Smith 1882

Haliporus Bate 1881:185 [part, excluding *Haliporus curvirostris* Bate 1881]. Bate 1888:284 [part]. Faxon 1893:213 [part]; 1895:189 [part]. Alcock 1901:22 [part]. Bouvier 1906b:1 [part]; 1908:78 [part]. A. Milne Edwards and Bouvier 1909:206 [part]. de Man 1911:31 [part]. Fowler 1912:542 [part].

Hymenopenaeus Smith 1882:91 [type-species by monotypy, *Hymenopenaeus debilis* Smith 1882. Gender, masculine. Placed on the Official List of Generic Names in Zoology as Name No. 1816, International Commission on Zoological Nomenclature (1969), Opinion 864]. Smith 1885: 179 [part]. Burkenroad 1936:102 [part]. Kubo 1949:212 [part]. Holthuis 1962:108. International Commission on Zoological Nomenclature 1969:139. Roberts and Pequegnat 1970: 29 [part].

Diagnosis.–Body slender, carapace elongate, integument thin, flexible. Rostrum variable in length, reaching between distal 0.25 of first antennular article and end of peduncle; ventral margin straight; usually armed only with dorsal teeth, occasionally also with ventral teeth; epigastric and first rostral teeth separated from remaining teeth by relatively long interval. Orbital spine absent; postorbital, antennal, hepatic, and branchiostegal spines present; pterygostomian spine present or absent. Cervical sulcus deep, long, extending to, but not across, middorsum of carapace; hepatic sulcus well marked; branchiocardiac carina sharp, accompanying sulcus deep; posthepatic and submarginal carinae present. Abdomen carinate dorsally at least along posterior three somites. Prosartema moderately long, flexible. Telson with pair of conspicuous fixed, lateral spines. Antennular flagella similar, filiform, and longer than carapace. Mandibular palp two-jointed, articles relatively narrow, distal one much shorter than basal, and tapering to blunt apex. First maxilla with unsegmented palp (endite of basis), gently narrowing to rounded apex. Fourth and fifth pereopods extremely long and flagelliform. First pereopod with spine on

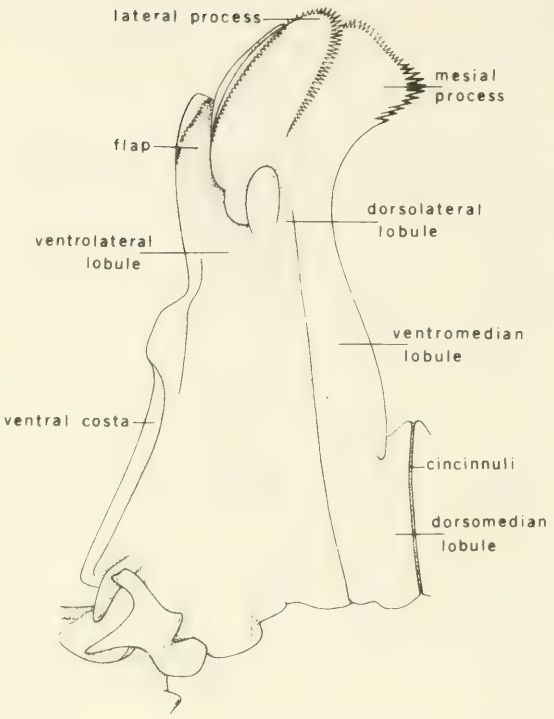

FIGURE 2.—Left half of petasma (dorsal view) of *Hymenopenaeus debilis* showing terms used in descriptions.

basis and usually on ischium. Exopods on all maxillipeds and pereopods. Lateral ramus of uropod armed with distolateral spine, reaching distal margin of lamella (terminal spine). In males, petasma with distal part of ventral costa fused to flexible flap of ventrolateral lobule; distal end of rib of dorsolateral lobule elevated above adjacent area and not projecting beyond distal margin; ventromedian lobule usually produced in conspicuous processes distally; endopod of second pleopod bearing appendices masculina and interna, and with basal sclerite produced distally into elongate, ventrolateral ("posterior") spur. Thelycum of open type, lacking enclosed seminal receptacle. Pleurobranchia present on somites IX to XIV; rudimentary arthrobranchia on somite VII, and anterior and posterior arthrobranchiae on somites VIII to XIII. Podobranchia present on second maxilliped, and epipod on second maxilliped (and on first if proximal exite of coxa considered an epipod) through fourth pereopod.

List of species.–Following are the species listed in each of the two sections proposed by Burkenroad (1936), a division with which I am in full agreement.

Section 1. Pterygostomian spine present.
Atlantic, Indo-West Pacific: *Hymenopenaeus laevis* (Bate 1881). Indo-West Pacific: *Hymenopenaeus sewelli* Ramadan 1938. Eastern Pacific: *Hymenopenaeus doris* (Faxon 1893); *Hymenopenaeus nereus* (Faxon 1893).

Section 2. Pterygostomian spine absent.
Atlantic: *Hymenopenaeus aphoticus* Burkenroad 1936; *Hymenopenaeus debilis* Smith 1882; *Hymenopenaeus chacei* Crosnier and Forest 1969. Indo-West Pacific: *Hymenopenaeus aequalis* (Bate 1881); *Hymenopenaeus fattahi* Ramadan 1938; *Hymenopenaeus halli* Bruce 1966; *Hymenopenaeus neptunus* (Bate 1888); *Hymenopenaeus obliquirostris* (Bate 1881); *Hymenopenaeus propinquus* (de Man 1907).

Affinities.–The members of the genus *Hymenopenaeus* differ from those of the closely related *Haliporoides, Pleoticus, Hadropenaeus* n. gen., and *Mesopenaeus* n. gen., in having a more slender body; a thin, flexible, almost membranous integument; the epigastric and first rostral teeth separated from the remaining teeth by an interval longer than the spaces between the more anterior teeth; and in possessing a posthepatic carina. They also differ from those of the other genera in having a slender mandibular palp in which the distal article is much shorter than the basal; extremely long and flagelliform fourth and fifth pairs of pereopods, and in certain features of the petasma: the terminal part of the ventrolateral lobule forms a flap to which the ventral costa is fused, the rib of the dorsolateral lobule is elevated distally from the surrounding area, and the ventromedian lobule is produced distally into conspicuous processes.

Remarks.–In the widely utilized work of Kubo (1949) several statements are made which should be discussed. Kubo based his description of the genus *Hymenopenaeus* primarily on two species found in Japanese waters [*H. lucasii* (Bate 1881) and *H. aequalis* (Bate 1888)], which led him to make erroneous generalizations. First, he considered the presence of two, instead of one, arthrobranchiae on somite VII as a character typical of *Solenocera,* and in his key to the genera of the subfamily Solenocerinae utilized this character to distinguish it from other genera in the subfamily. In at least one species (*Pleoticus robustus,* previously included in *Hymenopenaeus*), of a genus other than *Solenocera,* however, I find that there are two arthrobranchiae on somite VII. Secondly, Kubo noted that the petasma in *"Hymenopenaeus"* possessed spinules along the distal margin; actually, in some species they are absent. Finally, in the section "Arrangement of branchiae" Kubo indicated the restriction of podobranchia to somite VIII (on second maxilliped) in the members of the subfamily Solenocerinae, and in his table 6D he noted the presence of only one podobranchia in *Hymenopenaeus* and *Parahaliporus* (=*Haliporoides*). In the key to the genera of the subfamily, however, he utilized the occurrence of a rudimentary podobranchia on somites IX and X as the only feature to distinguish *Hymenopenaeus* from *Haliporus* and *Parahaliporus.* He used this feature in the key although in the following description of the genus *Hymenopenaeus,* he stated that in the specimens of *H. lucasii* and *H. aequalis* at his disposal, the epipods of none of the thoracic appendages behind the second maxilliped are furnished with podobranchia. It thus seems that in the key the line corresponding to *Hymenopenaeus* and the line corresponding to *Parahaliporus* and *Haliporus* were transposed; however, podobranchiae are present behind somite VIII in *Haliporus*

(at least on the third maxilliped and as far as the third pereopod) but not in *Parahaliporus*.

Key to Species of *Hymenopenaeus* in American Waters

1. Pterygostomian spine present (section 1) ..2
   Pterygostomian spine absent (section 2) ...4

2. Scaphocerite, at most, barely overreaching antennular peduncle. Rostrum, in adult, falling short of distal end of first article of antennular peduncle. Females with pyramidal, median protuberance on sternite XIV projecting ventrally. Males with ventromedian lobule of petasma bearing two or three small triangular processes distomesially .... *H. laevis*
   Scaphocerite overreaching antennular peduncle by, at least, 0.25 of its own length. Rostrum, in adult, surpassing distal end of first antennular article 3

3. Females lacking median protuberance on sternite XIV. Males with petasma bearing subrectangular distomesial process projecting at right angle to mesial margin, and armed with long spines ..... *H. nereus*
   Females with subpyramidal median protuberance on sternite XIV projecting anteroventrally. Males unknown . *H. doris*

4. Eye with cornea hemispherical and disposed such that imaginary line extending from mesial tubercle parallel to basal margin of ocular peduncle intersects lateral border of latter far proximal to proximolateral extremity of cornea ..... *H. aphoticus*
   Eye with cornea subreniform and disposed such that line extending from mesial tubercle parallel to basal margin of ocular peduncle intersects posterolateral extremity of cornea ..... *H. debilis*

Hymenopenaeus debilis Smith 1882

Figures 2, 3, 4B, 5-9

Hymenopenaeus debilis Smith 1882:91, pl. 15, fig. 6-11, pl. 16, fig. 1-3 [syntypes: 1 ♀, SE of Savannah Beach, Ga., 31°57′00″N, 78°18′35″W, 333 fm (609 m), 12 July 1880, *Blake* stn 317. 1 ♀, MCZ 3270, SE of Cape Fear, N.C., 33°19′00″N, 76°12′30″W, 457 fm (836 m), 14 July 1880, *Blake* stn 323. 1 ♀, USNM 4920, E of Cape Fear, N.C., 33°42′15″N, 76°00′50″W, 464 fm (849 m), 14 July 1880, *Blake* stn 326]. Smith 1887:687, pl. 16, fig. 7. Burkenroad 1936:111, fig. 63-64. Yokoya 1941:52. Anderson and Lindner 1945: 289. Harvey 1952:352. Ramadan 1952:9, fig. 22-23. Springer and Bullis 1956:7. Holthuis 1962: 108. Boschi 1964:38. Bullis and Thompson 1965:5. Zariquiey Alvarez 1968:47, fig. 24b. Crosnier and Forest 1969:545. International Commission on Zoological Nomenclature 1969: 139. Roberts and Pequegnat 1970:31. Pequegnat and Roberts 1971:8. Crosnier and Forest 1973:269, fig. 85 c-d, 87b, 89a.

Haliporus debilis. Faxon 1896:163. Bouvier 1905a:980; 1906a:253; 1906b:3; 1908:83, pl. 1, fig. 6, pl. 14, fig. 9-18. A. Milne Edwards and Bouvier 1909:206, pl. 2, fig. 8. de Man 1911:7. Fowler 1912:543. Boone 1927:78. Maurin 1961: 530; 1968:484. Vilela 1970:122.

Haliporus debilis var. *africanus* Bouvier 1908:83 [syntypes: 4 ♂ 3 ♀, MP, off Mazaghan, 33°46′N, 9°02′W, 1,319 m, 14 June 1883, *Talisman* stn 21].

Material

UNITED STATES—New Jersey: 1 ♀, USNM, Hudson Canyon, 550-600 m, 17 August 1972, *Gosnold* stn 123. 1 ♂, USNM, off Barnegat Inlet, 768 m, 3 August 1884, *Albatross* stn 2187. 1 ♂, USNM, N of Little Egg Inlet, 984 m, 19 August 1884, *Albatross* stn 2201. North Carolina: 6 ♂ 6 ♀, UNC-IMS, E of Cape Fear, 495-490 m, 29 July 1970, *Eastward* 19 stn 14954. 1 ♀ syntype, USNM 4920, E of Cape Fear, 849 m, 14 July 1880, *Blake* stn 326. 1 ♀ syntype, MCZ 3270, SE of Cape Fear, 836 m, 14 July 1880, *Blake* stn 323. 5 ♂ 4 ♀, USNM, SE of Cape Fear, 744 m, 6 May 1886, *Albatross* stn 2676. Georgia: 1 ♀, USNM, off St Catherines I, 814 m, 25 June 1961, *Atlantis* stn A-266-2. Florida: 4 ♀, USNM, NE of Cape Kennedy, 922 m, 3 May 1886, *Albatross* stn 2660. 6 ♂, USNM, NE of Cape Kennedy, 931 m, 3 May 1886, *Albatross* stn 2659. 3 ♀, USNM, SE of Key West, 558-514 m, 29 August 1967, *Gerda* stn 861. 1 ♀, USNM, off St Petersburg, 465 m, 29 September 1951, *Oregon* stn 489. 1 ♀, USNM, off Destin, 512 m, 14 March 1885, *Albatross* stn 2397. 1 ♂ 1 ♀, TAMU, off Santa Rosa I, 565 m, 4 August 1968, *Alaminos* stn 68A7-10A. 1 ♀, TAMU, off Gulf Beach, 1,061 m, 7 August 1968, *Alaminos* stn 68A7-13A. Alabama: 2 ♀, USNM, off Orange Beach, 585 m, 13 August 1970, *Oregon II* stn 11146. 1 ♂ 5 ♀, USNM, S of Mobile Bay, 366 m, 18 December 1962, *Oregon* stn 4151. Louisiana: 1 ♂ 1 ♀, USNM, E of Mississippi Delta, 439-448 m, 17 July 1960, *Oregon* stn 2825. 1 ♀, USNM, E of Southeast Pass, Mississippi Delta, 626 m, 11 February 1885, *Albatross* stn 2376. 3 ♀, TAMU, off Garden I Bay, Mis-

sissippi Delta, 476 m, 15 October 1969, *Alaminos* stn 69A13-40. 1 ♂ 7 ♀, USNM, E of Mississippi Delta, 457 m, 10 June 1959, *Silver Bay* stn 1203. 1 ♂ 1 ♀, MCZ, SE of Mississippi Delta, 587 m, 1878, *Blake* stn 47. 28 ♂ 121 ♀ 110 juv and larvae, YPM, S of Grand Terre Is, 302 m, 26 March 1936, *Atlantis* stn 2381. 1 ♀, YPM, S of Grand Isle, 356 m [in *Atlantis* log 300 fm, 549 m], 23 March 1937, *Atlantis* stn 2831. 6 ♂ 11 ♀, USNM, SW of Ship Shoal Lighthouse, 549 m, 23 February 1964, *Oregon* stn 4709. Texas: 1 ♀, TAMU, off Port Aransas, 476 m, 19-20 November 1968, *Alaminos* stn 68A13-22. 2 ♀, USNM, off Padre I, 585-658 m, 20 July-6 August 1969, *Western Gulf* stn 35. 1 ♀, USNM, off Padre I, 501 m, 21 March 1969, *Oregon II* stn 10456.

MEXICO—Tamaulipas: 1 ♀, TAMU, SW of Matamoros, 713 m [according to label], 12 November 1968, *Alaminos* stn 68A13-3. 1 ♀, TAMU, SW of Matamoros, 878 m, 12 November 1968, *Alaminos* stn 68A13-1. Quintana Roo: 2 ♀, USNM, off Cabo Catoche, 585 m, 13 August 1970, *Oregon II* stn 11146.

BAHAMA ISLANDS—1 ♀, RMNH, NW of Matanilla Reef, 662-702 m, 18 July 1965, *Gerda* stn 671. 2 ♂ 5 ♀, RMNH, NW of Great Stirrup Cay, 733-897 m, 4 July 1963, *Gerda* stn 190. 1 ♂, USNM, off Dog Rocks, Cay Sal Bank, 618 m, 22 June 1967, *Gerda* stn 815.

GREATER ANTILLES—1 ♂ 4 ♀, USNM, N of Puerto Rico, 732-658 m, 30 January 1933, Johnson-Smithsonian Deep-Sea Exp., stn 1. 1 ♀, USNM, N of Puerto Rico, 476 m, 4 February 1933, Johnson-Smithsonian Deep-Sea Exp., stn 23. 1 ♂, USNM, N of Puerto Rico, 512 m, 4 February 1933, Johnson-Smithsonian Deep-Sea Exp., stn 24. 1 ♀, RMNH, SW of Navassa I, Jamaica Channel, 1,034 m, 2 July 1970, *Pillsbury* stn 1187.

LESSER ANTILLES—1 ♂ 5 ♀, USNM, SW of Sombrero I, 664-704 m, 23 July 1969, *Pillsbury* stn 989. 1 ♂ 2 ♀, USNM, off Dog I, 688 m, 6 December 1969, *Oregon II* stn 10834. 1 ♀, USNM, W of Dog I, 658 m, 10 December 1969, *Oregon II* stn 10847. 5 ♀, USNM, W of Saba Bank, 786 m, 3 December 1969, *Oregon II* stn 10833. 1 ♂ 3 ♀, USNM, E of Standfast Pt, Antigua, 786-1,125 m, 18 July 1969, *Pillsbury* stn 954. 2 ♀, USNM, Guadeloupe Passage, 738-832 m, 17 July 1969, *Pillsbury* stn 946. 1 ♀, USNM, off Point du Nord, Marie Galante I, 704-732 m, 12 July 1969, *Pillsbury* stn 919. 3 ♂ 14 ♀, USNM, E of Capesterre, Guadeloupe I, 549-686 m, 14 July 1969, *Pillsbury* stn 923. 8 ♀, USNM, off Dominica I, 808 m, 5 March 1966, *Oregon* stn 5930. 2 ♀, USNM, off Dominica I, 607 m, 4 March 1966, *Oregon* stn 5927. 2 ♂ 3 ♀, USNM, off Vieux Fort, St Lucia, 417-589 m, 9 July 1969, *Pillsbury* stn 904. 2 ♂, USNM, NE of Soufrière, St Vincent, 576-842 m, 6 July 1969, *Pillsbury* stn 881.

BELIZE—2 ♂ 4 ♀, YPM, N of Glover Reef, 885 m, 20 March 1925, *Pawnee*.

NICARAGUA—5 ♀, USNM, off Punta de Perlas, 613 m, 22 November 1968, *Oregon II* stn 10207.

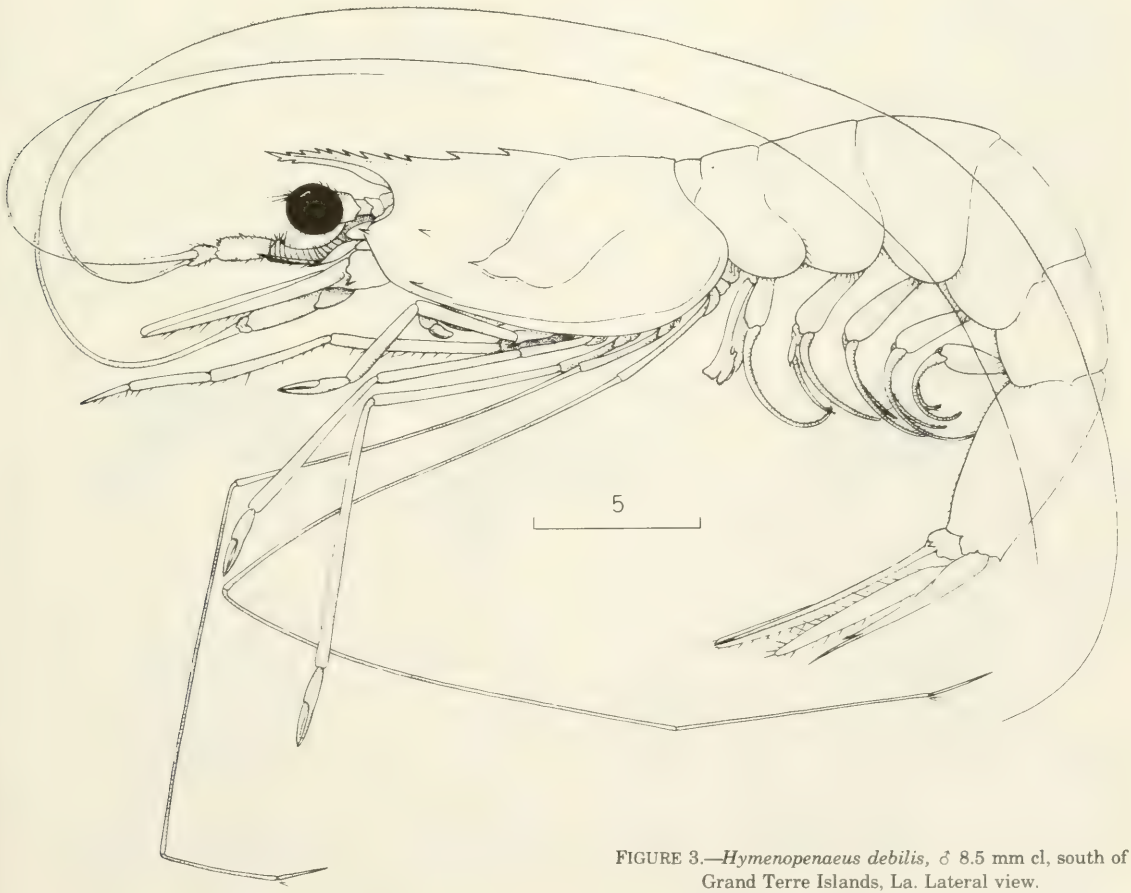

FIGURE 3.—*Hymenopenaeus debilis*, ♂ 8.5 mm cl, south of Grand Terre Islands, La. Lateral view.

PANAMA—1 ♀, RMNH, Golfo de los Mosquitos, 664-681 m, 21 July 1966, *Pillsbury* stn 447.

COLOMBIA—1 ♀, USNM, Golfo del Darién, 731 m, 28 May 1964, *Oregon* stn 4902.

VENEZUELA—1 ♀, USNM, E of San Juan de los Cayos, 421 m, 9 October 1963, *Oregon* stn 4439.

GUYANA—1 ♀, USNM, N of Fort York, 1,373-1,446 m, 15 July 1968, *Pillsbury* stn 689.

AZORES ISLANDS—1 ♀, MP, between Pico and São Jorge, 1,257 m, 15 August 1883, *Talisman* stn 139.

MOROCCO—4 ♂ 3 ♀ syntypes of *Haliporus debilis* var. *africanus* Bouvier, MP, off Mazaghan, 1,319 m, 14 June 1883, *Talisman* stn 21. 1 ♂ 9 ♀, MP, off Cap Cantin, 1,590 m, 17 June 1883, *Talisman* stn 33.

Description.–Body slender, integument thin, flexible and glabrous (Figure 3). Rostrum straight or slightly to strongly upturned, moderately long, reaching as far as distal end of second antennular article, its length not greater than 0.55 that of carapace, low and with dorsal and ventral margins straight. Rostral plus epigastric teeth $\frac{8\text{-}11}{0\text{-}4}$ (usually $\frac{9\text{-}10}{2}$, only 3% lacking ventral teeth); epigastric tooth located at about 0.4 cl from orbital margin, first rostral tooth (largest of all) at about 0.3 cl, and third above orbital margin; ventral teeth variously arranged, either closely grouped together or rather broadly spaced. Adrostral carina low and sharp, extending from orbital margin almost to apex of rostrum; orbital margin projecting anteroventrally in narrow shelf. Postrostral carina strong to just caudal to cervical sulcus, weak posteriorly, and followed by minute dorsal tubercle very near margin of carapace. Lateral spines on carapace slender and sharp: postorbital spine situated directly posterior to antennal and almost as long as branchiostegal; latter (largest of all) continuous with short, sharp basal carina; pterygostomian spine absent. Cervical carina sharp, cervical sulcus deep, extending to, but not crossing, postrostral carina, its dorsal extremity located at 0.55 cl from orbital margin, or slightly more posteriorly; hepatic sulcus with two ventral convexities, extending from below hepatic spine to anterior end of branchiocardiac sulcus; weak posthepatic carina extending posteriorly from junction of latter sulci. Branchiocardiac carina strong, accompanying sulcus moderately deep; submarginal carina slender, extending along entire length of branchiostegite.

Eye (Figure 4B) with basal article produced mesially into small scale. Cornea broad, its greatest diameter approximately twice that of base of ocular peduncle (1.6-2.1, $\bar{x}$ 1.95; $N = 32$), and proportion of diameter to carapace length varying between 15.5 and 23.0, $\bar{x}$ 19.7. Cornea subreniform, with proximal margin oblique, slanting posterolaterally; an imaginary line drawn parallel to base of short ocular peduncle at level of its mesial tubercle intersects cornea.

Antennular peduncle length equivalent to about 0.55 that of carapace; prosartema short, not quite reaching distomesial margin of cornea, falling short of distal margin of first antennular article, but its long distal setae overlapping base of second article; stylocerite rather short, its length about 0.6 of distance between its proximal extrem-

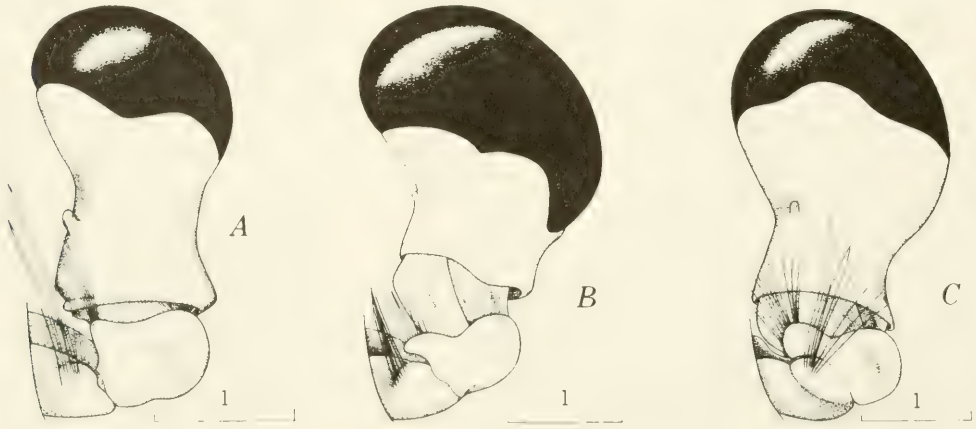

FIGURE 4.—Eyes. *A, Hymenopenaeus laevis,* ♀ 21 mm cl, off Martha's Vineyard, Mass. *B, Hymenopenaeus debilis,* ♂ 10.5 mm cl, northwest of Great Stirrup Cay, Bahama Islands. *C, Hymenopenaeus aphoticus,* ♀ 18 mm cl, northwest of Península de la Guajira, Colombia.

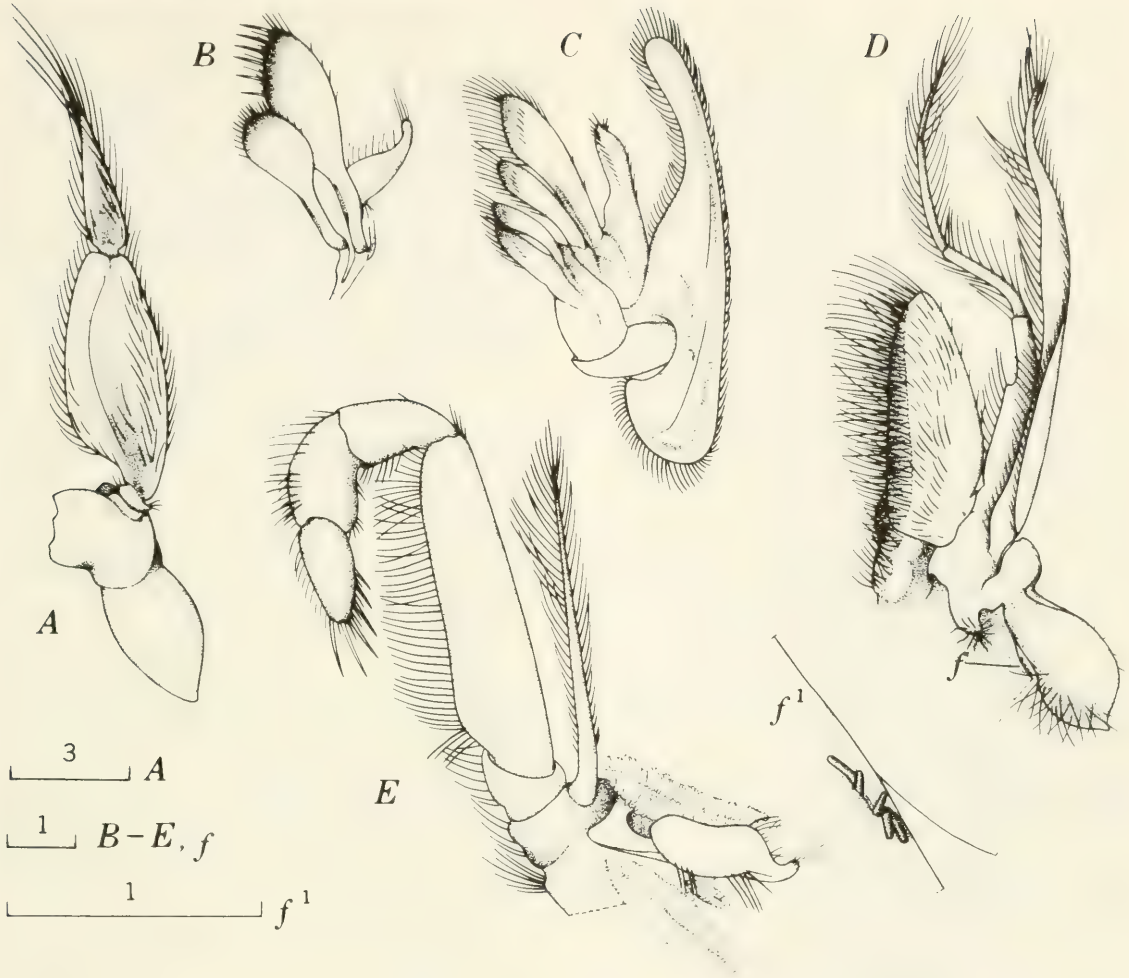

FIGURE 5.—*Hymenopenaeus debilis*, ♀ 19.5 mm cl, off Cape Kennedy, Fla. *A*, Mandible. *B*, First maxilla. *C*, Second maxilla. *D*, First maxilliped. *E*, Second maxilliped. *f*, Rudimentary arthrobranchia. f^1, Enlargement of *f* (all from left side).

ity and mesial base of distolateral spine; latter long, slender, and sharp. Antennular flagella very long and considerably unequal in length, ventral 2.15 and dorsal 7.5 times carapace length in shrimp 7 mm cl, and 1.7 and 5.5 times, respectively, in shrimp 10 mm cl. Scaphocerite overreaching antennular peduncle by as much as 0.25 of its own length; lateral rib ending in slender spine, falling short to slightly surpassing distal margin of lamella. Antennal flagellum incomplete in all specimens examined; however, in one individual about 35 mm tl, antennal length 155 mm, thus not less than 4.4 times total length of shrimp.

Mandibular palp (Figure 5*A*) reaching to about level of distal 0.2 of carpocerite; proximal article 2.4 times as long as wide; distal article considerably shorter and narrower than proximal, and tapering to blunt tip. First and second maxillae, and first and second maxillipeds as illustrated (Figure 5*B-E*, virtually identical throughout genus); somite VII bearing rudimentary arthrobranchia at base of first maxilliped (Figure 5*Df-f*^{1}). Third maxilliped overreaching antennular peduncle by length of dactyl and propodus; length of dactyl about 0.7 that of propodus.

First pereopod, stoutest of five, reaching distal end of carpocerite or surpassing it by as much as length of dactyl. Second pereopod overreaching antennular peduncle by at least half length of dactyl or by entire propodus. Third pereopod exceeding antennular peduncle by length of dactyl,

propodus, and as much as 0.4 that of carpus. Fourth pereopod reaching beyond antennular peduncle by length of last three podomeres. Fifth pereopod exceeding antennular peduncle by length of last three podomeres or by latter and as much as 0.1 length of merus. Pereopods increasing in length from first to fifth. First pereopod with rather inconspicuous spine on basis, and either slender spine or no spine on ischium; second pereopod with small spine on basis. In female, coxa of third pereopod produced into large subtrapezoidal plate directed mesially, and bearing minute anteromesial spine in juveniles. In both sexes spine present on anteromesial corner of coxa of fifth pereopod, considerably stronger in males than in females, spine minute in latter and borne on rounded coxal plate.

Abdomen with middorsal carina from fourth through sixth somites, posterodorsal margin of fourth and fifth with short median incision; sixth somite about 1.8 times as long as high, bearing small, sharp spine at posterior end of carina, and pair of minute spines posteroventrally. Telson with rather shallow median sulcus practically disappearing before reaching level of base of lateral spines; sulcus flanked by ridges, blunt anteriorly, sharp and slender posteriorly; terminal portion length 5-6 times basal width; lateral spines length 1.5-2.0 times basal width of terminal portion. Mesial ramus of uropod falling short of apex of telson or slightly overreaching it; lateral ramus overreaching mesial ramus by as much as 0.25 of its own length, and armed with slender, distolateral spine, reaching as far as contiguous margin of ramus.

Petasma (Figures 2, 6*A, B*) with row of cincinnuli (hooklike structures along mesial margin of median lobes of petasma that serve to interlock its two halves) occupying only proximal 0.3 of median line, and entire terminal margin armed with spines; ventromedian lobule deeply cleft distally forming two elongate processes: mesial one subspatulate and armed with rather conspicuous spines mesially and minute ones distolaterally; lateral process subelliptical, raised inwardly in elongate prominence, and produced proximally in small auricular process lacking spinules; distal flap of ventrolateral lobule extending only to basal portion of lateral process, and turned strongly outward; ventral costa forming low prominence at base of, and imperceptibly merging with, flap.

Appendix masculina (Figure 6*C, D*) elevated in sharp mesial ridge and with proximal part produced laterally into rounded, flattened lobe; distal part narrowing and bearing lateral row of setae terminating in apical tuft of longer ones. Appendix interna elongate ovate, extending almost as far as appendix masculina, and also armed with apical tuft of setae. Ventrolateral spur of basal sclerite long, its length 0.7-0.8 that of appendix masculina.

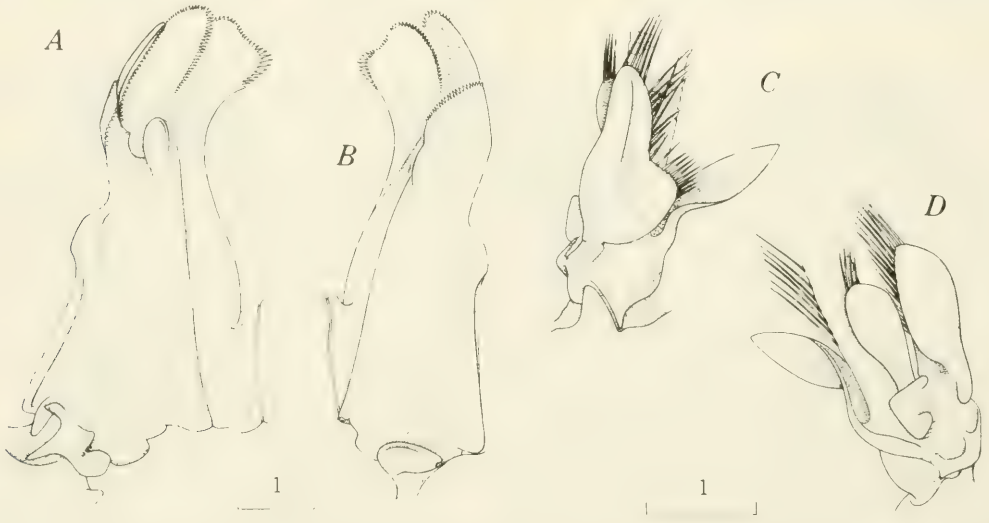

FIGURE 6.—*Hymenopenaeus debilis*, ♂ 13 mm cl, off Cape Kennedy, Fla. *A*, Petasma, dorsolateral view of left half. *B*, Ventral view. *C*, Right appendices masculina and interna, dorsolateral view. *D*, Ventral view.

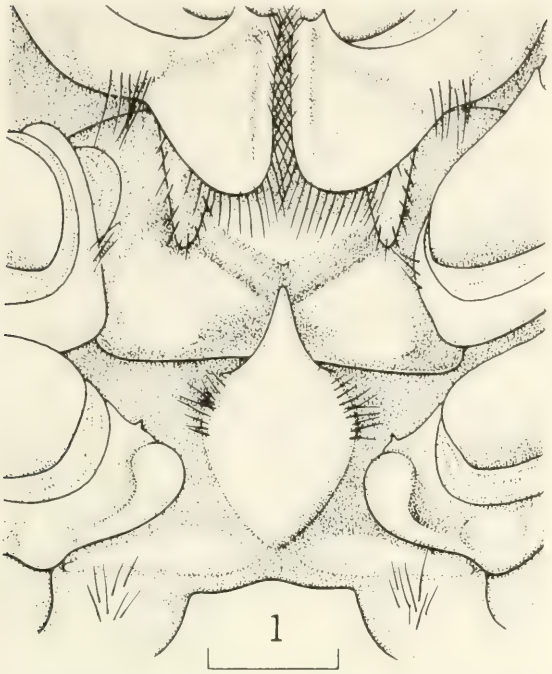

FIGURE 7.—*Hymenopenaeus debilis*, ♀ 15.5 mm cl, Dominica Island, Lesser Antilles. Thelycum, ventral view.

Thelycum (Figure 7) with median protuberance on sternite XIV pyriform, strongly produced anteriorly into acute, freely projecting apical portion overlapping, and closely appressed to, sternite XIII; latter bearing paired subtriangular elevations with bases raised in horizontal ridges flanking tip of protuberance on sternite XIV; anterior part of sternite XIII with setose transverse prominence; sternite XII bearing pair of large, setose, posterolateral horns reaching or slightly surpassing midlength of sternite XIII.

Photophores.–Six present on sternum: pair in elevated posterior margin of sternite XIII, just mesial to coxae of fourth pereopods; pair between second pleopods; single one between bases of fourth pereopods, and another between bases of fifth pleopods. Details of their structure given by Burkenroad (1936).

Color.–Bouvier (1908) on the basis of a water color illustration made at the moment of capture stated that the color is "d'un rouge-orange presque uniform." Burkenroad (1936) described fresh material as "transparent, speckled with minute scarlet chromatophores which were concentrated at the bases of the pleopods and uropods and at the tip of the telson. The ocular peduncle at the base of the cornea, the mouthparts, and the tip of the second maxillipede were scarlet. The stomach was red, the pleonic gut and nerve-cord orange; the gastric gland brownish, the ovary creamy (as seen through the overlying tissues). The eyes were reddish brown."

Maximum size.–Males, 55 mm tl; females, 78 mm tl (Bouvier 1908). Largest specimens examined by me: males 15.5 mm cl, 52 mm tl; females, 19.5 mm cl, 75 mm tl.

Geographic and bathymetric ranges.–Western Atlantic: from Hudson Canyon, New Jersey (39°55′N, 70°31′W) through the Gulf of Mexico and Caribbean Sea to Guyana (08°14′N, 57°38′W). Eastern Atlantic: Azores Islands and northwest Africa—from Cap Spartel, Morocco, to Cape Verde Islands, including Canary Islands (Figure 8). It has been found at depths (Figure 9) between 300 and 2,163 m (latter in Bouvier 1908).

Affinities.–Hymenopenaeus debilis closely resembles *H. aphoticus,* but differs from it in that the rostrum is usually armed with ventral teeth (only 3% of the specimens examined by me lack such teeth), and the sternum bears six photophores which are absent in *H. aphoticus.* The cornea is subreniform, and it is disposed such that its proximal margin is oblique to the basal margin of the ocular peduncle and an imaginary line extending from the medial tubercle parallel to the basal margin of the peduncle crosses its proximolateral extremity. The cornea (actually the entire eye) of *H. debilis* is also much larger than that of *H. aphoticus:* its maximum diameter about twice that of the basal margin of the peduncle, and the proportion of the diameter to the carapace length ranges from 15.5 to 22.0, averaging 19.7. Furthermore, in males of *H. debilis* the petasma exhibits larger distal processes than does that of *H. aphoticus,* but the lateral one is produced proximally in an auricle which is small and unarmed, and the proximomesial spinules on the free margin of the mesial process are only slightly longer than the remaining ones instead of considerably so as in *H. aphoticus.* Finally, the length of the ventrolateral spur borne by the sclerite at the base of the appendices masculina and interna is equivalent to 0.50-0.75 that of the appendix masculina. The thelyca of the two species are

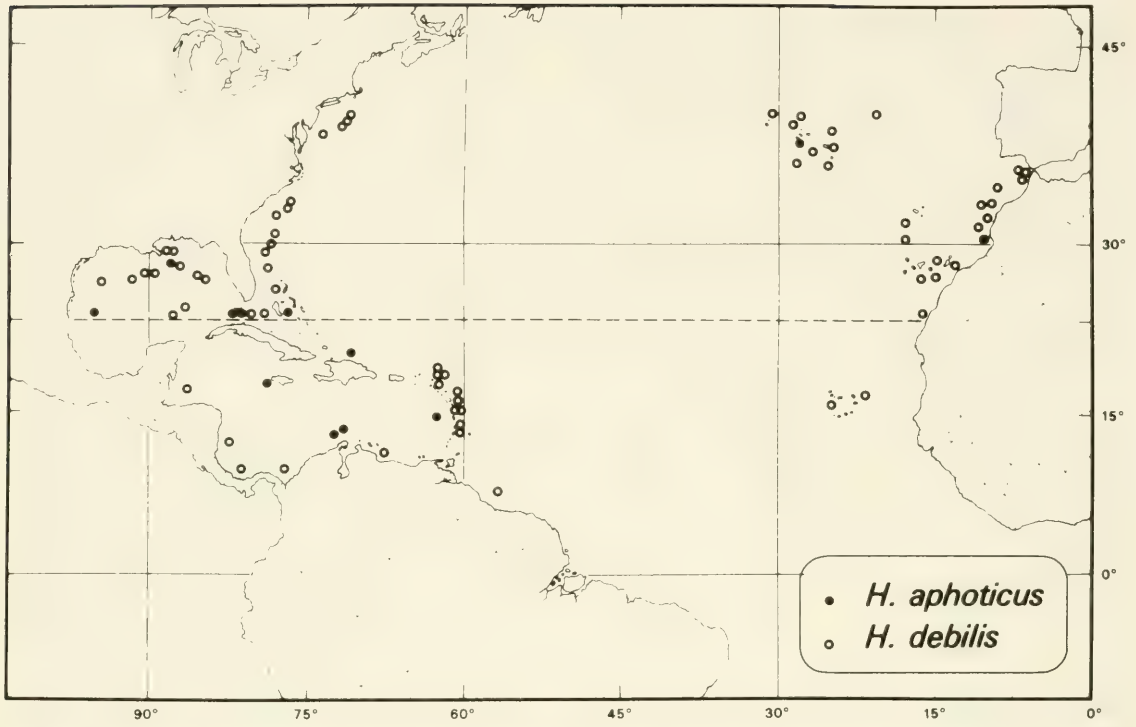

FIGURE 8.—Ranges of *Hymenopenaeus aphoticus* and *Hymenopenaeus debilis* based on published records and specimens personally examined.

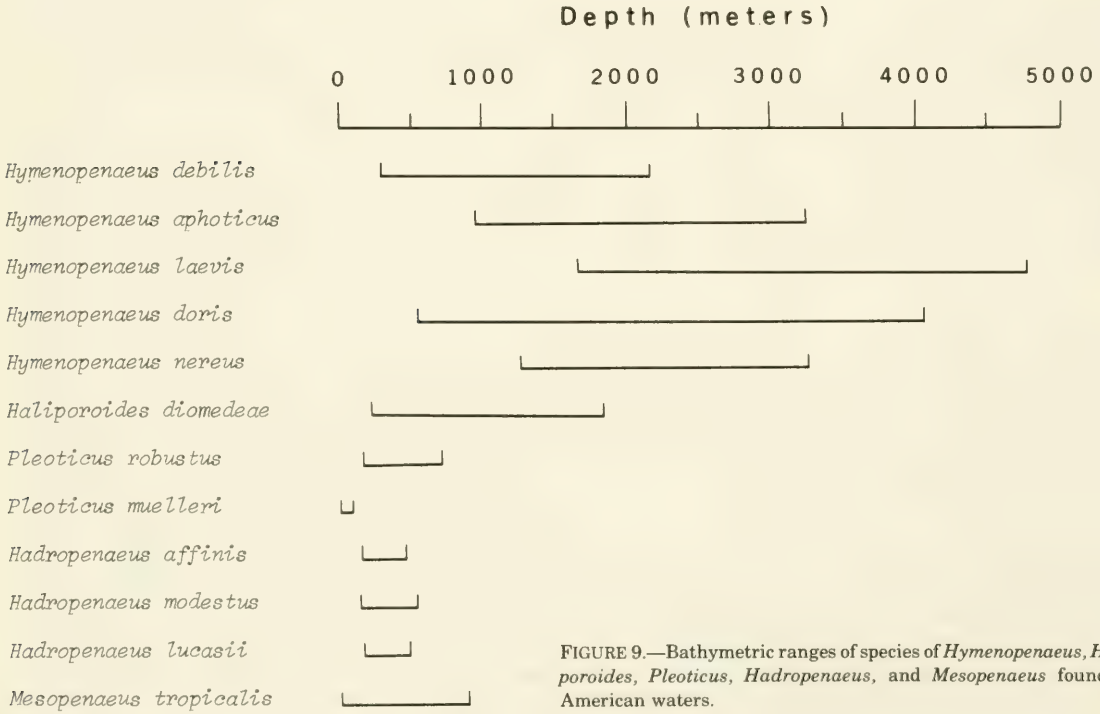

FIGURE 9.—Bathymetric ranges of species of *Hymenopenaeus*, *Haliporoides*, *Pleoticus*, *Hadropenaeus*, and *Mesopenaeus* found in American waters.

similar but the median protuberance of sternite XIV tends to be broader in *H. debilis* than in *H. aphoticus*.

According to Burkenroad (1936), in this species the proportion of the maximum diameter of the eye to carapace length is even greater than that given above, ranging between 19.3 and 26.9, $\bar{x}$ 22.3. My measurements of specimens studied by Burkenroad resulted in proportions not exceeding 23.0. This could be due to a slight reduction of the cornea caused by the preservatives, or the cornea is now deformed in the specimens with larger corneae examined by me.

Very similar to *H. debilis* is *H. chacei* which is known only from off West Africa. According to Crosnier and Forest (1969, 1973), these two species differ in that in *H. chacei* the ventral border of the rostrum is unarmed (actually, as stated above, 3% of the individuals of *H. debilis* examined by me lack such teeth), and no photophores are present. The cornea of *H. chacei* is narrower than that of *H. debilis*, in the former the ratio of the greatest diameter to the carapace length ranges from 13.2 to 16.0 ($\bar{x}$ 15.0), and it is disposed such that its proximolateral extremity lies slightly distal to the level of the medial tubercle.

A careful study of the western Atlantic specimens in which the rostrum is ventrally unarmed has left no doubt in my mind that they are *H. debilis*. *Hymenopenaeus chacei*, which typically lacks teeth on the ventral margin of the rostrum, is not represented in the extensive collections from the western Atlantic examined by me.

I have found that in males of *H. debilis* the disposition of both the mesial and lateral processes of the petasma varies from slightly to rather strongly inclined mesially, the former illustrated herein (Figure 6*A*, *B*), and the latter, illustrated by Crosnier and Forest (1973, plate 85, figure c-d, a male from Morocco). This variation is not associated with the size of the animal, and occurs throughout the entire range of the species in the western Atlantic. Males in which the processes are only slightly inclined mesially resemble those of *H. chacei* in which, according to Crosnier and Forest (1973), the roughly angular portion of the lateral process is typically directed forward. The males of the two species can still be distinguished by the size and armature of the auricular process of the petasma, which in *H. debilis* is very small and unarmed but relatively large in *H. chacei* and provided with marginal spinules (Crosnier and Forest 1969:546, figure 2).

Remarks.–The coordinates of the *Talisman* stations, cruise of 1883, where the material examined by me was collected, are given herein according to the data presented by Crosnier and Forest (1973).

The disposition of the third syntype, from southeast of Savannah Beach, Ga., caught at *Blake* stn 317 is unknown.

Hymenopénaeus aphoticus Burkenroad 1936

Figures 4C, 8-12

Hymenopenaeus aphoticus Burkenroad 1936:112, fig. 62, 65, 66, 67 [holotype: ♀, YPM 4556; type-locality: Turks Is Passage, 1,646-1,728 m, 21°15′40″N, 71°17′06″W, *Pawnee* stn 54]. Yokoya 1941:52. Crosnier and Forest 1969:547.

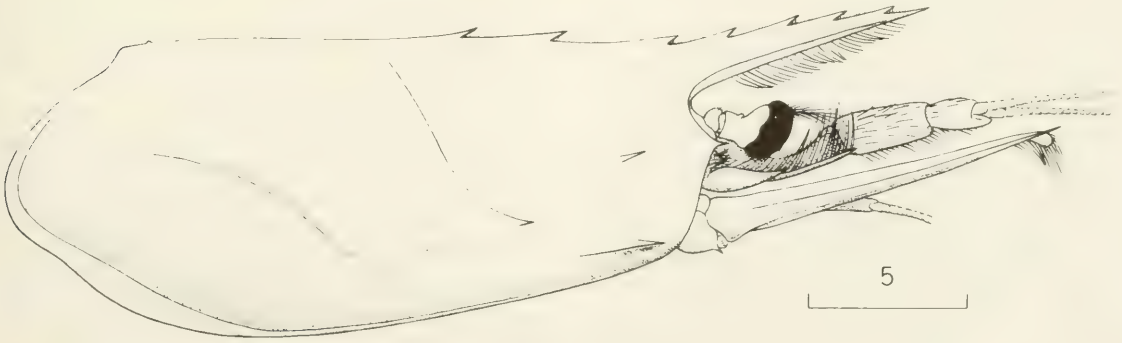

FIGURE 10.—*Hymenopenaeus aphoticus*, ♀ 18 mm cl, northwest of Península de la Guajira, Colombia. Cephalothorax, lateral view.

Roberts and Pequegnat 1970:31, fig. 3-1D. Pequegnat and Roberts 1971:8. Crosnier and Forest 1973:253, fig. 85e-f, 87c, 88b, 89c.

Material

UNITED STATES—Florida: 5 ♂ 3 ♀, RMNH-UMML, SW of Marquesas Keys, 1,373-1,428 m, 1 December 1964, *Gerda* stn 449. 2 ♂, USNM, SW of Marquesas Keys, 948-969 m, 29 August 1967, *Gerda* stn 858. 2 ♂, TAMU, NW of Dry Tortugas, 3,256 m, 29-30 July 1968, *Alaminos* stn 68A7-4E. 1 ♂, TAMU, SW of Cape San Blas, 1,097 m, 1 August 1968, *Alaminos* stn 68A7-7B. Alabama: 1 ♂, USNM, off Mobile Bay, 2,160 m, 3 March 1885, *Albatross* stn 2383. Texas: 1 ♀, TAMU, off Padre I, 1,399 m, 7 August 1969, *Alaminos* stn 69A11-7.

MEXICO—Tamaulipas: 1 ♀, USNM, off Boca de San Rafael, 1,668 m, 24 January 1970, *Oregon II* stn 10881. Veracruz: 1 ♂ 3 ♀, TAMU, NE of Tuxpan, 1,326 m, 24 August 1969, *Alaminos* stn 69A11-83. 1 ♂, TAMU, Bahía de Campeche, 2,122 m, 16 August 1969, *Alaminos* stn 69A11-44.

BAHAMA ISLANDS—1 ♂ paratype, YPM 4557, Tongue of the Ocean, "Wire 7000 feet" [2,134 m], 2 March 1927, *Pawnee* stn 11. ♂ holotype 1 ♀ paratype, YPM 4556, Turks I Passage, 1,646-1,728 m, 12 March 1927, *Pawnee* stn 54.

JAMAICA—1 ♀, USNM, W of South Negril Point, 1,591-1,829 m, 8 July 1970, *Pillsbury* stn 1238.

EASTERN CARIBBEAN—1 ♂ 6 ♀, USNM, S of I Aves, 1,249 m, 27 January 1884, *Albatross* stn 2117.

COLOMBIA—10 ♂ 6 ♀, USNM, NW of Península de la Guajira, 1,500 m, 27 July 1966, *Pillsbury* stn 454. 3 ♀, USNM, off Península de la Guajira, 2,500 m, 27 July 1966, *Pillsbury* stn 455.

Description.–Rostrum (Figure 10) slightly to rather strongly upturned, reaching as far as distal margin of second antennular article, its length about 0.45 that of carapace, and with both margins almost straight. Rostral plus epigastric teeth 7-8, sharp; epigastric tooth located at about 0.4 cl from orbital margin, first tooth (largest of all) at about 0.25, and second with apex at level of orbital margin; ventral teeth absent. Adrostral carina low and sharp, extending from orbital margin almost to apex of rostrum; orbital margin projecting anteroventrally in narrow shelf. Postrostral carina strong to just caudal to cervical sulcus, from there weak or indistinct porteriorly, and followed by minute tubercle located close to margin of carapace. Spines on lateral surface of carapace slender and sharp: postorbital spine situated directly posterior to antennal, and branchiostegal, largest of all, continuous with short, sharp carina; pterygostomian spine absent. Cervical sulcus deep, extending to, but not crossing, postrostral carina, its dorsal extremity placed at about 0.54 cl (or slightly farther anteriorly) from orbital margin; hepatic sulcus biconvex ventrally, running from base of hepatic spine to ventral end of branchiocardiac sulcus; weak posthepatic carina extending posteriorly from junction of latter sulci. Branchiocardiac sulcus long, accompanying carina strong. Submarginal carina slender.

Eye (Figure 4*C*) with basal article produced mesially into small scale. Cornea comparatively narrow, its greatest diameter approximately 1.5 times that of base of ocular peduncle (1.25-1.75, $\bar{x}$ 1.55; N = 20), and proportion of diameter to carapace length varying between 10.0 and 12.5, $\bar{x}$ 11.1. Cornea hemispherical, with proximal margin subperpendicular to longitudinal axis of elongate ocular peduncle; an imaginary line drawn parallel to base of ocular peduncle at level of its mesial tubercle intersects lateral border far proximal to cornea.

Antennular peduncle length equivalent to about 0.5 that of carapace; prosartema short, extending only as far as distomesial margin of cornea, falling short of distal margin of first antennular article, but with long distal setae reaching base of second antennular article; stylocerite moderately long, extending 0.60-0.65 of distance between its proximal extremity and mesial base of distolateral spine; latter rather long, slender, and sharp. Antennular flagella long and unequal in length, ventral one 2.25 times as long as carapace in shrimp 17.5 mm cl; dorsal flagellum longer than ventral, unfortunately incomplete in all specimens examined. Scaphocerite length approximately 3.65 times maximum width, overreaching antennular peduncle by as much as 0.3 of its own length; lateral rib ending in slender spine extending to, or slightly surpassing, distal margin of lamella. Antennal flagellum long, at least 6.8 times total length of shrimp: male with total length of 45 mm bearing incomplete flagellum 300 mm long. Mandibular palp, maxillae and first two maxillipeds similar to those in *H. debilis* (see Figure 5). Third maxilliped overreaching antennular peduncle by length of dactyl and propodus or by their lengths plus 0.1 that of carpus; length of dactyl about 0.7 that of propodus.

First pereopod, stoutest of five, reaching about distal end of carpocerite. Second pereopod overreaching antennular peduncle by, at least, tip of dactyl, or by as much as length of propodus. Third pereopod exceeding antennular peduncle by length of propodus and, at most, 0.4 that of carpus. Fourth pereopod overreaching antennular peduncle by length of distal three podomeres. Fifth pereopod exceeding antennular peduncle by length of distal three podomeres, or by length of

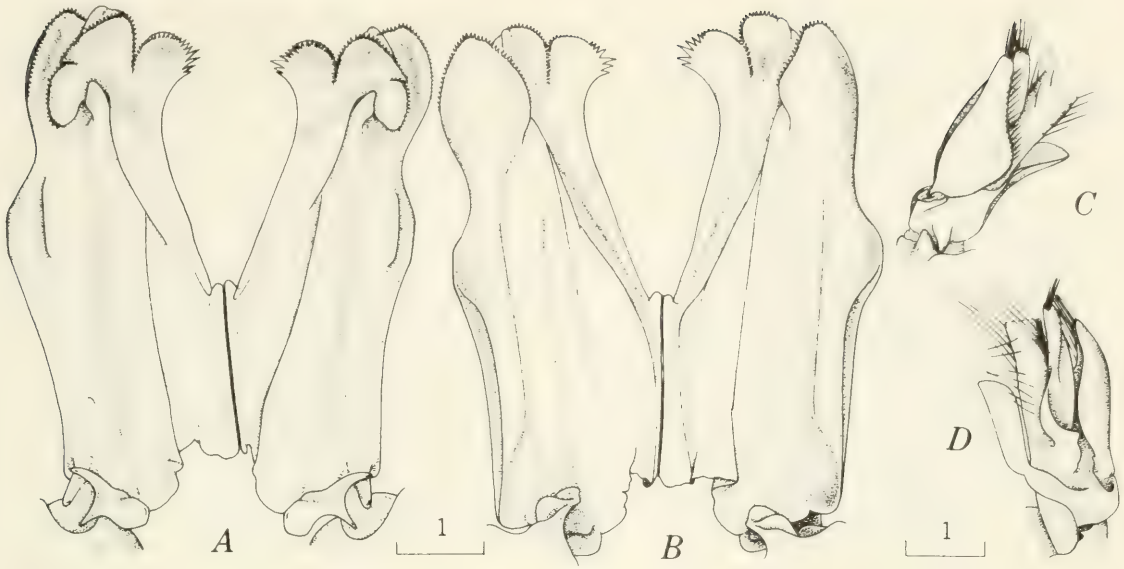

FIGURE 11.—*Hymenopenaeus aphoticus*, ♂ 14.5 mm cl, south of Isla Aves, eastern Caribbean. *A*, Petasma (extended), dorsolateral view. *B*, Ventral view. *C*, Right appendices masculina and interna, dorsolateral view. *D*, Ventromesial view.

those podomeres and as much as 0.15 length of merus. Pereopods increasing in length from first to fifth. First pereopod with rather inconspicuous spine on basis, and long slender spine on ischium; second pereopod with small spine on basis. In female, coxa of third pereopod produced into subtrapezoidal plate, latter broadest mesially, disposed almost at right angle to podomere, and bearing minute anteromesial tooth in juvenile. In both sexes, tooth present on anteromesial angle of coxa of fifth pereopod, considerably stronger in male than in female, in latter tooth minute and borne on rounded coxal plate.

Abdomen with middorsal carina from fourth through sixth somites, posterodorsal margin of fourth and fifth with short median incision; sixth somite about 1.8 times as long as high, bearing small, sharp spine at posterior end of carina and pair of minute spines posteroventrally. Telson with rather shallow median sulcus extending posteriorly to level of base of lateral spines, and flanked by well-developed ridges; terminal portion length 5-6 times its basal width; lateral spines length 1.4-1.7 times basal width of terminal portion. Mesial ramus of uropod falling short of, or slightly overreaching, apex of telson; lateral ramus overreaching mesial ramus by as much as 0.25 of its own length, and armed with small, slender distolateral spine, falling slightly short of, or barely overreaching, contiguous margin of ramus.

Petasma (Figure 11*A*, *B*) with row of cincinnuli occupying proximal 0.4 of median line, and entire terminal margin armed with spines; ventromedian lobule distally cleft forming two moderately long processes: mesial one subtrapezoidal and armed with conspicuous spines mesially and minute ones distolaterally, lateral process subelliptical, raised inwardly in strong prominence, and produced proximally in rather large auricular process armed with marginal spinules; distal flap of ventrolateral lobule free, extending as far distally as lateral process, and only slightly turned outward; ventral costa forming low prominence at, and imperceptibly merging with, base of flap.

Appendix masculina (Figure 11*C*, *D*) strongly elevated along mesial portion and with proximal part produced laterally into rounded, flattened lobe; distal part narrowing and bearing lateral row of setae continuous with apical tuft of long setae. Appendix interna elongate-ovate, extending slightly farther distally than appendix masculina, and armed with apical tuft of setae. Ventrolateral spur short, its length not greater than 0.5 that of appendix masculina.

Thelycum (Figure 12) similar to that of *H. debilis* (see above).

FIGURE 12.—*Hymenopenaeus aphoticus*, ♀ 18.5 mm cl, south of Isla Aves, eastern Caribbean. Thelycum, ventral view.

Maximum size.–Males: 18 mm cl; females: 19.5 mm cl.

Geographic and bathymetric ranges.–Western Atlantic: southwest Florida (23°56′N, 82°13′W), throughout the Gulf of Mexico, and the Caribbean Sea (12°55′N, 72°04′W). Eastern Atlantic (according to Crosnier and Forest 1973): south of the Azores Islands and off Morocco (Figure 8). It occurs at depths between about 950 m and 3,256 m (Figure 9).

Affinities.–Hymenopenaeus aphoticus is closely allied to *H. debilis,* but may be readily distinguished from it by the lack of teeth on the ventral margin of the rostrum, the absence of photophores, and the shape and disposition of the cornea (see above). In males of *H. aphoticus,* the petasma exhibits smaller distal processes than does that of *H. debilis,* and the auricle of the distolateral process is larger and armed with marginal spinules; also the proximomesial spinules on the free margin of the mesial process are considerably longer than the remaining ones, instead of only slightly longer as in *H.debilis.* Furthermore, in *H. aphoticus* the length of the ventrolateral spur at the base of the appendices masculina and interna is equivalent to only 0.5 that of the appendix masculina. Although the petasmata of the two species are different, the thelyca are markedly similar: the only detectable distinction is that the median protuberance on sternite XIV tends to be narrower in *H. aphoticus* than in *H. debilis.*

Remarks.–In examining a lot of seven specimens of *H. aphoticus* obtained at *Albatross* stn 2117, Roberts and Pequegnat (1970) misread the number on the accompanying label. They stated that in the Smithsonian Institution there is a lot of *H. aphoticus* taken by the *Albatross* at "Stn 2217, 1889" in the western Atlantic. Actually, the number on the label is 2117 for which the coordinates are 15°24′40″N, 63°31′30″W (south of Isla Aves in the eastern Caribbean, visited by the *Albatross* in 1884) instead of 2217, an 1889 station situated at 39°47′20″N, 69°34′15″W, which is off New Jersey. Because the authors thought the lot had been obtained at the latter locality, they stated that the species ranges as far north as 39°47′ (actually it has not been recorded from off the Atlantic coast of the United States). The misreading of the label also caused them to be unaware of the Caribbean record for *H. aphoticus* and to state that "It may eventually be found in the Caribbean also."

Hymenopenaeus laevis (Bate 1881)

Figures 4A, 9, 13-16

Haliporus laevis Bate 1881:185 [syntypes: 2 ♀, BMNH; type-locality: SW of Sierra Leone (W of Cameroon), 2°25′N, 20°01′W, 2,500 fm (4,573 m), *Challenger* stn 104]. Bate 1888:289, pl. 42, fig. 2. Bouvier 1906b:3; 1908:80. de Man 1911:7. Estampador 1937:494.

Hymenopenaeus microps Smith 1884:413, pl. 10, fig. 1 [syntypes: 1 ♀, USNM 7148, E of Georges Bank, Mass., 41°13′00″N, 60°00′50″W, 906 fm (1,657 m), *Albatross* stn 2076; 1 ♀ oral appendages, YPM 4559, off New Jersey, 38°50′00″N, 69°23′30″W, 1,731 fm (3,166 m), *Albatross* stn 2037]. Smith 1886:189; 1887:688, pl. 16, fig. 8. Wood-Mason 1891:277. Wood-Mason and Alcock 1891:188.

Haliporus microps. Alcock and Anderson 1894: 146. Alcock 1901:25. Bouvier 1906a:255; 1906b: 3; 1908:80. de Man 1911:7. Fowler 1912:543.

Hymenopeneus microps. Alcock 1899a:30.

Haliporus androgynus Bouvier 1906a:253 [syntypes: 1 ♀, MP, between "Dakar et la Praya," (off Mauritania), 16°38′N, 20°44′W, 3,200 m, *Talisman* stn 105. 1 ♀, MP, between "Dakar et

la Praya," (off Senegal), 15°48′N, 20°23′W, 3,655 m, *Talisman* stn 106]. Bouvier 1906b:3; 1908:80. de Man 1911:7.

Haliporus sp. Lenz and Strunck 1914:300, fig. 2.

Hymenopenaeus laevis. Burkenroad 1936:106; 1938:61. Anderson and Lindner 1945:289.Crosnier and Forest 1973:253, fig. 82a, 83b.

Material

UNITED STATES—Massachusetts: 1 ♀ syntype of *H. microps* Smith, USNM 7148, E of Georges Bank, 1,657 m, 4 September 1883, *Albatross* stn 2076. 1 ♀, USNM, SE of Martha's Vineyard, 2,844 m, 30 July 1883, *Albatross* stn 2042. New Jersey: 1 ♀, USNM, off Atlantic City (Hudson Canyon), 1,977 m, 9 August 1885, *Albatross* stn 2550. 1 ♀ [oral appendages] syntype of *H. microps* Smith, YPM 4559, 3,166 m, 18 July 1883, *Albatross* stn 2037. Virginia: 4 ♀, USNM, 1 ♀, AMNH, E of Delmarva Peninsula, 4,792 m, 29 August 1885, *Albatross* stn 2566. North Carolina: 1 ♀ 1 ♀, USNM, NE of Kitty Hawk, 4,708 m, 8 September 1884, *Albatross* stn 2224.

BERMUDA ISLANDS—1 ♂, YPM, N of Bermuda Is, "10000 feet wire" [3,048 m], 20 April 1927, *Pawnee* stn 58. 1 ♀, YPM, N of Bermuda Is, "8000 feet wire" [2,438 m], 21 April 1927, *Pawnee* stn 59.

BAHAMA ISLANDS—1 ♂ 2 ♀, YPM, Turks I Passage, "8000 feet wire" [2,438 m], 11 April 1927, *Pawnee* stn 52. 2 ♀, YPM, Turks I Passage, "6500 feet wire" [1,981 m], 13 April 1927, *Pawnee* stn 56.

MAURITANIA—1 ♀ syntype of *H. androgynus* Bouvier, MP, between "Dakar et la Praya" [off Mauritania], 3,200 m, 18 July 1883, *Talisman* stn 105.

SENEGAL—1 ♀ syntype of *H. androgynus* Bouvier, MP, between "Dakar et la Praya" [off Senegal], 3,655 m, 19 July 1883, *Talisman* stn 106.

CAMEROON—2 ♀ syntypes, BMNH, "south-west of Sierra Leone," 2°25′N, 20°1′W [W of Cameroon], 4,573 m, 23 August 1873, *Challenger* stn 104.

PHILIPPINE ISLANDS—1 ♀, BMNH, off Manila, 1,920 m, 13 November 1874, *Challenger* stn 205.

Description.–Rostrum (Figure 13) short, its length about 0.2 that of carapace, falling short of distal margin of first antennular article, horizontal or slightly upturned, tapering to very sharp tip, and with ventral margin slightly sinuous. Rostral plus epigastric teeth 7-9, sharp; epigastric tooth situated at about 0.4 cl from orbital margin, first rostral tooth (largest of all) at approximately 0.3, and third opposite to, or slightly forward of, orbital margin. Adrostral carina low and sharp, extending from orbital margin almost to apex of rostrum; orbital margin projecting anteroventrally in narrow shelf. Postrostral carina well defined to near posterior margin of carapace, followed by small tubercle. Pterygostomian spine small; postorbital (situated directly posterior to relatively small antennal spine), branchiostegal, and pterygostomian spines continuous with sharp basal carina. Cervical carina sharp, notched dorsal to hepatic spine; cervical sulcus deep, extending to, but not crossing postrostral carina, its dorsal extremity located at or slightly posterior to midlength of carapace; hepatic carina blunt, its accompanying sulcus deep; additional short carina lying dorsal and parallel to posterior part of hepatic sulcus; posthepatic carina long, running almost to posterior margin of carapace; branchiocardiac carina also long, virtually reaching posterior margin of carapace; short sulcus extending posterodorsally from near posterior end of branchiocardiac carina; submarginal carina well defined, extending along entire length of branchiostegite.

Eye (Figure 4*A*) with basal article produced mesially into barely distinct scale; ocular peduncle long; cornea comparatively narrow, its greatest diameter about 1.4 times that of base of ocular peduncle, its proximal margin only slightly slanting posterolaterally.

Antennular peduncle length equivalent to about 0.55 that of carapace; prosartema short, extending only as far as distomesial margin of cornea, falling considerably short of distal margin of first antennular article; stylocerite short, extending only 0.4-0.5 of distance between its prox-

FIGURE 13.—*Hymenopenaeus laevis*, ♀ 12.5 mm cl, Turks Island Passage, Bahama Islands. Cephalothorax, lateral view.

imal extremity and mesial base of distolateral spine; latter long, slender, and sharp. Antennular flagella incomplete in all specimens examined by me, according to Bate (1888) "about two-thirds the length of the animal." Scaphocerite reaching as far as antennular peduncle or barely overreaching it; lateral rib ending in slender spine falling slightly short of, or slightly overreaching, distal margin. Antennal flagellum broken in specimens examined by me, according to Bate (1888) "rather longer than the animal." Mandibular palp reaching to about distal 0.25 of carpocerite. Third maxilliped overreaching antennular peduncle by length of dactyl and propodus; length of dactyl about 0.75 that of propodus.

First pereopod extending to about distal end of carpocerite. Second pereopod reaching distal end of antennular peduncle, or exceeding it by as much as length of dactyl. Third pereopod surpassing antennular peduncle by length of dactyl, propodus, and at least 0.25 that of carpus. Fourth pereopod exceeding antennular peduncle by length of dactyl, propodus, and 0.4-0.5 that of carpus. Fifth pereopod overreaching antennular peduncle by length of dactyl, propodus, and 0.75-0.80 that of carpus. Pereopods increasing in length from first to fifth. First pereopod with minute spine on basis, and small one on ischium; second pereopod with small spine on basis. Coxal plate of third pereopod in females broadening mesially and produced posteriorly into setose, rounded lobe. Tooth present on anteromesial corner of coxa of fifth pereopod in both sexes, strong and blunt in males, minute, and borne by rounded coxal plate in females.

Abdomen with middorsal carina from fourth through sixth somites, posterodorsal margin of fourth and fifth with short median incision, sometimes bearing minute spine at base; sixth somite about twice as long as high, armed with small, sharp spine at posterior end of carina and pair of posteroventral spines. Telson with median sulcus deep anteriorly, increasingly shallower posteriorly to level of base of lateral spines, flanked by paired ridges, blunt anteriorly, sharp posteriorly; length of terminal portion about 5 times its basal width; spines moderately long, 1.20-1.35 basal width of terminal portion. Mesial ramus of uropod falling short of apex of telson, or overreaching it by no more than 0.1 of its length; lateral ramus exceeding mesial ramus by as much as 0.2 of its own length, and armed with small, terminal, distolateral spine.

Petasma (Figure 14*A*, *B*) with row of cincinnuli occupying about proximal 0.5 of median line, its entire terminal margin lacking spines; ventromedian lobule bearing two, rarely three, small, triangular processes distomesially, and short,

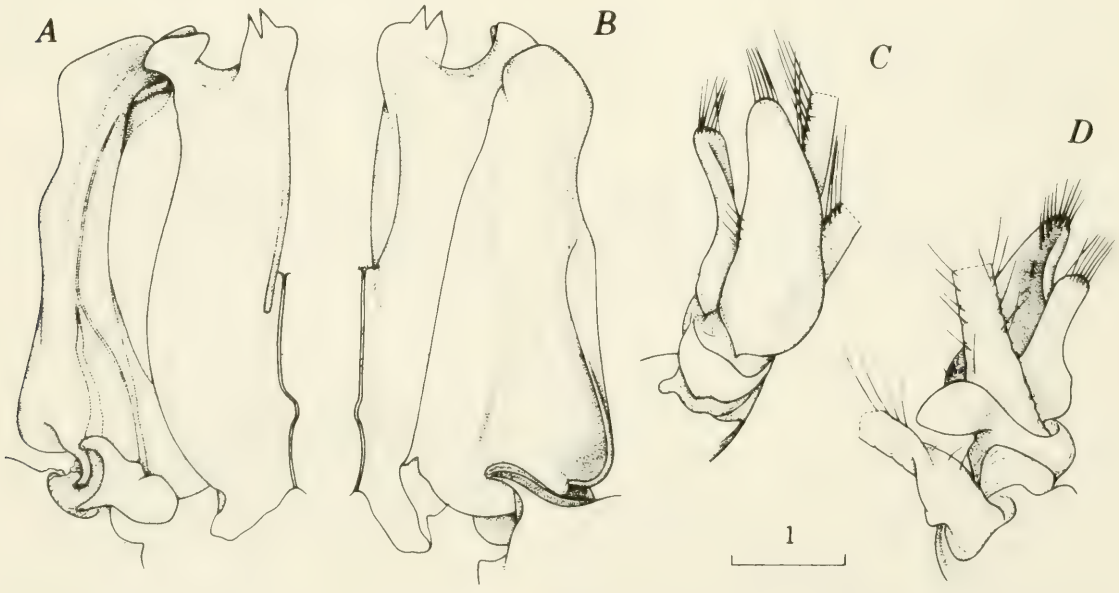

FIGURE 14.—*Hymenopenaeus laevis*, ♂ 15 mm cl, Turks Island Passage, Bahama Islands. *A*, Petasma, dorsolateral view of left half. *B*, Ventrolateral view. *C*, Right appendices masculina and interna, dorsolateral view. *D*, Ventromesial view.

rigid, transversely elliptical process distolaterally; distal part of ventrolateral lobule roughly elliptical and strongly trending toward ventromedian lobule; ventral costa broad proximally, considerably narrower distally and, in young, ending in minute marginal spine projecting from base of elliptical part of ventrolateral lobule.

Appendix masculina (Figure 14*C, D*) with proximal part produced laterally into rounded lobe bearing row of long setae on distal margin continuous with row extending along midventral line of narrow distal portion; latter armed with apical tuft of long setae; appendix interna abruptly narrowing from rounded base and bearing apical tuft of long setae; ventrolateral spur with distal part subovate, bearing longitudinal submarginal rib on dorsal surface.

Thelycum (Figure 15) with median protuberance on sternite XIV setose, pyramidal, and with triangular base, its apical portion produced into short ventrally directed projection; median lamella projecting vertically from posterior margin of sternite XIII, flat, its distal margin slightly to deeply emarginate (emargination angular or curved), lateral margins straight or slightly concave; posterior part of sternite XII bearing paired, setose horns overreaching midlength of sternite XIII.

Maximum size.–Males: 15 mm cl; females: 22 mm cl.

Geographic and bathymetric ranges.–Western Atlantic: from off Georges Bank, Mass. (41°13′00″N, 60°00′50″W), to the Bahamas (21°20′15″N, 71°13′20″W), including the Bermudas (Figure 16). Eastern Atlantic: from west of Mauritania to off Equatorial Guinea (Bate 1888). Indo-West Pacific: in the Arabian Sea (Laccadive Sea, Wood-Mason and Alcock 1891), the Bay of Bengal (off Andaman Islands,Wood-Mason 1891; Alcock 1901), and the Philippines (Bate 1888). If the record of "*Haliporus* sp." by Lenz and Strunck (1914) is actually one for this species, its range off west Africa reaches farther south, at least to off Liberia (0°39′N, 18°57′W). This shrimp has been found at depths between 1,657 and 4,792 m (Figure 9). Its habitat together with its small size are most probably responsible for the few collections available.

Affinities.–Hymenopenaeus laevis is closely allied

FIGURE 15.—*Hymenopenaeus laevis*, ♀ 17 mm cl, Turks Island Passage, Bahama Islands. Thelycum, ventral view.

to the American Pacific *H. doris* and *H. nereus*, and to the Indo-West Pacific *H. sewelli*. These four species form the compact section 2 of Burkenroad's group IV. They are the only members of the genus which possess both branchiostegal and pterygostomian spines.

Females of *H. laevis* differ strikingly from those of *H. nereus* in the structure of the thelycum. In those of *H. nereus*, the median lamella of sternite XIII is directed anteriorly, and has arched or sinuous lateral margins converging basally. Furthermore, in *H. nereus* the median lamella is flanked by paired, caudally inclined processes, which are lacking in *H. laevis*, and sternite XIV is raised in a median longitudinal ridge, very different from the strong pyramidal prominence present in the latter. This shrimp, in turn, can be separated readily from *H. doris* by the median lamella of

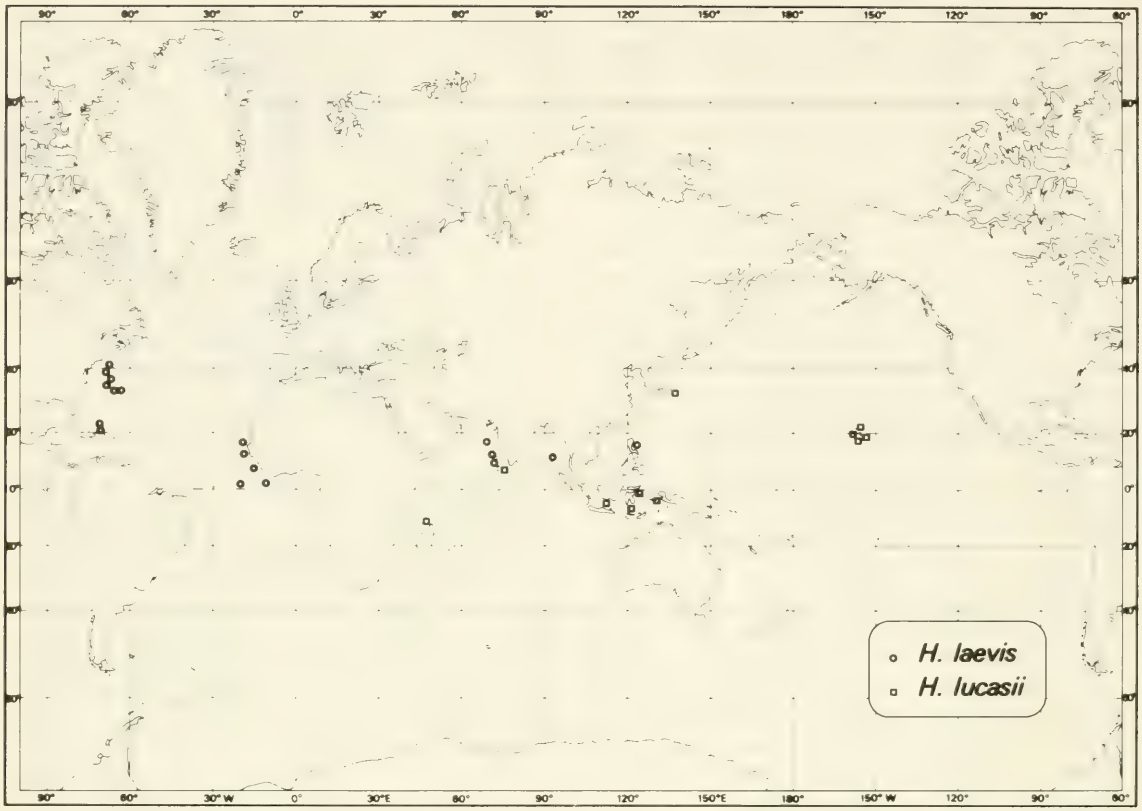

FIGURE 16.—Ranges of *Hymenopenaeus laevis* and *Hadropenaeus lucasii* based on published records and specimens personally examined.

sternite XIII which in the latter is concave anteriorly, has a usually convex, never emarginate, distal margin. The median lamella also is flanked by paired ridges which are triangular in cross section and as high as the lamella. Furthermore, in *H. doris*, sternite XIV bears a median protuberance which is strongly produced in an elongate projection lying quite close to the lamella.

Males of *H. laevis* differ markedly from those of *H. nereus* in that the petasma of the latter bears a single, large, mesial process distally which, moreover, is subrectangular, directed perpendicular to the main axis of the petasma, and armed with long spines; in addition, the lateral process is directed distomesially instead of extending transversely, and is strongly curved outward. Finally, the distal part of the ventrolateral lobule of the petasma is acuminate instead of subelliptical, and is only slightly inclined toward the ventromedian lobule.

As previously indicated by Burkenroad (1936) and Crosnier and Forest (1973), females of this species exhibit considerable variation in the shape and size of the median lamella on sternite XIII. Extending ventrally, it may be short or long, reaching between midheight and slightly beyond the apex of the median protuberance on sternite XIV. In the young, the lamella is truncate, and in the adult it ranges from shallow to deeply emarginate distally, forming a fork with the projections varying from rather broadly triangular to spinelike.

In the young male, as stated above, the petasma bears a minute subdistal spine at the free margin of the costa, and the more mesial of the two distal projections of the ventromedian lobule is at best only slightly developed.

Remarks.–Burkenroad (1936) presented a detailed account of the external morphology and an enlightened analysis of the taxonomic status of this species; as a result, he placed two well-known scientific names, *H. microps* and *H. androgynus*,

in the synonymy of *H. laevis*. In this same contribution, Burkenroad mentioned a "minute denticle of variable size" posterior to the epigastric tooth, and suggested that it is "probably the remains of the larval anterior dorsal organ." In that location, however, I have observed nothing more than an extremely slight elevation of the postrostral carina, and that only in two specimens. Had this feature not been mentioned by Burkenroad, I should have overlooked it, and, after observing it, I believe it to be insignificant.

Bouvier (1906b) described *Haliporus androgynus* on the basis of two specimens which bear, in addition to a fully developed thelycum, both petasma and appendices masculinae. Burkenroad (1936) stated that the simultaneous presence of the female and male external genitalia in these specimens probably represents an abnormality. Recently, Crosnier and Forest (1973) indicated that this combination of secondary sexual characters could represent an expression of protandric hermaphroditism, as reported by Heegaard (1967) in *Solenocera membranacea* (Risso 1816). They added that in a rather large number of penaeids the maximum size of males corresponds to the minimum size of females. It should be noted, however, that Burkenroad (1936) cited a female of *H. laevis*, also examined by me, with a carapace length of 8 mm, which is about half the length of the largest known male, 15 mm cl.

In the two syntypes of *H. androgynus*, which have a carapace length of about 20 mm, the petasmata are shorter than in other males of equal size, and exhibit and armature with these juvenile features. In one of the specimens, the mesial projection is extremely small, whereas the lateral projection and the distolateral process are well developed; in the other, the mesial projection is distinct, the lateral one very small, the distolateral process is well developed, and a subdistal spine is present on the free margin of the ventral costa.

Hymenopenaeus doris (Faxon 1893)

Figures 9, 17, 18A, 19-20

Haliporus doris Faxon 1893:214 [syntypes: 4 ♀, MCZ 4648, off Cabo Velas Costa Rica, 10°14′N, 96°28′W, 2,232 fm (4,082 m), 8 April 1891, *Albatross* stn 3414. 1 ♀, USNM 21182, S of Punta Maldonado, Guerrero, Mexico, 14°46′N, 98°40′W, 1,879 fm (3,437 m), 10 April 1891, *Albatross* stn 3415]. Faxon 1895:191, pl. 49, fig. 1-1c. Bouvier 1906b:3; 1908:80. de Man 1911:7

Hymenopenaeus doris. Burkenroad 1936:104; 1938:60. Crosnier and Forest 1973:256, fig. 83d.

Aliporus doris. del Solar C. 1972:4.

Material

MEXICO—Territorio de Baja California: 1 ♀, USNM, off Punta Chivato, Golfo de California, 1,567 m, 20 March 1889, *Albatross* stn 3009. 1 ♀, AMNH, 54 km off Punta Arena, mouth of Golfo de California, 914 m, 29 April 1936, Templeton Crocker Expedition stn 159 T-3 [station data from Beebe 1937].

COSTA RICA—4 ♀ syntypes, MCZ 4648, off Cabo Velas, 4,082 m, 8 April 1891, *Albatross* stn 3414. 1 ♀, USNM, off Cabo Velas, 4,082 m, 8 April 1891, *Albatross* stn 3414.

Description.–Rostrum (Figure 17) relatively short, its length about 0.2 that of carapace, reaching between base and midlength of second antennular article, upturned, tapering to sharp tip, and with ventral margin straight. Rostral plus epigastric teeth 7-8, sharp; epigastric tooth situated about 0.4 cl from orbital margin, first rostral tooth (largest of all) at approximately 0.3, and base of

FIGURE 17.—*Hymenopenaeus doris*, syntype ♀ 32.5 mm cl, off Cabo Velas, Costa Rica. Cephalothorax, lateral view.

third in line with orbital margin. Adrostral carina low and sharp, extending from orbital margin almost to apex of rostrum; orbital margin projecting in narrow shelf. Postrostral carina strong to near posterior margin of carapace, followed by small tubercle. Pterygostomian spine slender and sharp like other lateral spines on carapace; postorbital (situated directly posterior to antennal), pterygostomian, and branchiostegal spines with sharp basal carina, that continuous with branchiostegal spine merging with hepatic carina. Cervical carina strong, extending to, but not crossing, postrostral carina, its dorsal extremity located immediately posterior to midlength of carapace; hepatic carina blunt, its accompanying sulcus deep; additional short carina lying dorsal and parallel to posterior part of hepatic sulcus; posthepatic carina long, running from posterior extremity of hepatic sulcus to posterior margin of carapace; branchiocardiac carina also long, reaching posterior margin of carapace; short sulcus extending posterodorsally from near posterior end of branchiocardiac carina; submarginal carina well defined, extending along entire length of branchiostegite.

Eye as illustrated (Figure 18*A*).

Antennular peduncle length equivalent to about 0.4 that of carapace; prosartema extending to distal margin of eye, but falling short of distal end of first antennular article; stylocerite short, extending 0.5 of distance between its proximal extremity and mesial base of distolateral spine; latter rather long, slender, and sharp. Antennular flagella incomplete in specimens examined.

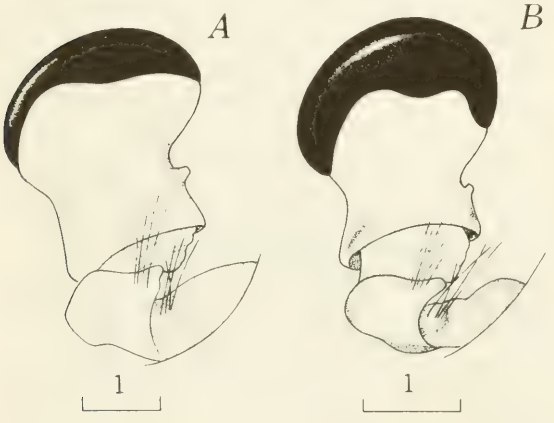

FIGURE 18.—Eyes. *A, Hymenopenaeus doris*, syntype ♀ 32.5 mm cl, off Cabo Velas, Costa Rica. *B, Hymenopenaeus nereus*, syntype ♀ 21.5 mm cl, south of Cabo Blanco, Costa Rica.

Scaphocerite overreaching antennular peduncle by 0.25 of its own length; lateral rib ending in slender spine, extending to distal margin of lamella. Antennal flagellum broken in specimens studied. Mandibular palp reaching distal 0.2 of carpocerite; proximal article about 2.5 times as long as wide; distal article considerably shorter and narrower than proximal, and tapering to blunt tip. First maxilliped with single rudimentary arthrobranchia at base. Third maxilliped reaching beyond antennular peduncle by dactyl and almost entire length of propodus; length of dactyl about 0.65 that of propodus.

First pereopod extending to distal end of carpocerite. Second pereopod overreaching antennular peduncle by length of propodus. Third pereopod exceeding antennular peduncle by length of propodus and about 0.33 that of carpus. Fourth pereopod overreaching antennular peduncle by dactyl, propodus, and almost entire length of carpus. Fifth pereopod reaching beyond antennular peduncle by length of distal three podomeres. Pereopods increasing in length from first to fifth. First pereopod with rather inconspicuous spine on basis, and slender spine on ischium; second pereopod with minute spine on basis. In female, coxa of third pereopod produced into large, subtrapezoidal plate, broadest mesially, and disposed almost at right angle to podomere; coxa of fifth pereopod armed with minute anteromesial tooth.

Abdomen with middorsal keel from fourth through sixth somites, and strong longitudinal rib along lateral surface of fourth and fifth somites; posterodorsal margin of latter two somites with short median incision; sixth somite very elongate, 2.5 times as long as high, bearing small, sharp spine at posterior end of keel and pair of minute posteroventral spines. Telson with broad median sulcus deep anteriorly, quite shallow posteriorly, and flanked by low, sharp ridges; terminal portion length 5-6 times basal width; lateral spines short, their length about 1.5 times basal width of terminal portion. In only specimen with complete uropod, mesial ramus falling short of apex of telson; lateral ramus overreaching mesial ramus by 0.2 of its own length, and armed with small, terminal, distolateral spine.

Petasma unknown; males not recorded.

Thelycum (Figure 19*A, B*) with median protuberance on sternite XIV subpyramidal, with subtriangular base and apical portion strongly produced into elongate, acute projection directed ventrally or anteroventrally, and lying quite near

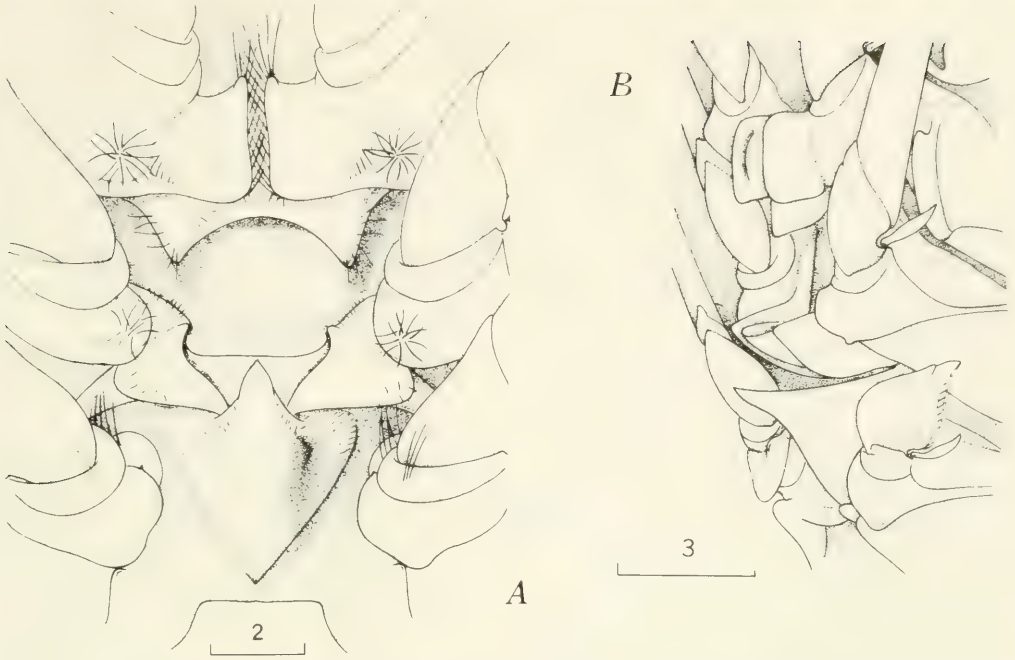

FIGURE 19.—*Hymenopenaeus doris,* syntype ♀ 32.5 mm cl, off Cabo Velas, Costa Rica. *A,* Thelycum,ventral view. *B,* syntype ♀ 32 mm cl, same locality, thelycum, ventrolateral view (setae omitted).

median lamella of sternite XIII; lamella, projecting vertically, heavily sclerotized, excavate anteriorly, with distal margin truncate or convex; pair of high ridges (triangular in cross section) flanking and posteriorly overlapping median lamella; posterior part of sternite XII bearing paired short, blunt horns covered by long setae.

Maximum size.–Females: 33.5 mm cl.

Geographic and bathymetric ranges.–Eastern Pacific: from off Punta Chivato (27°09′N, 111°42′W), Gulf of California, to Isla del Coco, Costa Rica (Figure 20), at depths between 549 and 4,082 m (Figure 9). Burkenroad (1938) cited the depth, 300 fm (549 m), at which one juvenile specimen was taken from the *Arcturus* off Isla del Coco, but did not give the coordinates of the locality. Beebe (1926), however, indicated that the various hauls from the *Arcturus* in the area were made slightly south of Isla del Coco, and cited the following coordinates: 4°30′N, 87°00′W.

Affinities.–Hymenopenaeus doris is closely allied to *H. nereus,* the only other member of the genus known from the American Pacific. Females of the two species can be distinguished readily by thelycal features: in *H. doris* a strong median protuberance is present on sternite XIV, and the lamella on the posterior margin of sternite XIII is disposed vertically, is deeply excavate anteriorly, and its distal margin is truncate or convex; in *H. nereus* only a median longitudinal rib is present on sternite XIV, and the lamella on XIII is inclined anteriorly, is flattened, and its distal margin is concave. Finally, in *H. doris* the lamella is flanked by high ridges whereas in *H. nereus* these are replaced by flattened, scalelike processes directed caudally.

Remarks.–Only nine specimens of *H. doris* are known. Seven, five of which are syntypes, were collected by the *Albatross* (1891); one of these (not designated by Faxon as part of the type-series) was taken with four syntypes at *Albatross* stn 3414, and the seventh was caught in the Gulf of California at *Albatross* stn 3009. Two additional specimens were cited by Burkenroad (1938), a juvenile female from the mouth of the Gulf of California, and another juvenile from off Isla del Coco (Costa Rica) taken by the *Arcturus* in 300 fm (549 m).

FIGURE 20.—Ranges of *Hymenopenaeus doris*, *Hymenopenaeus nereus*, and *Haliporoides diomedeae* based on published records and specimens personally examined.

Hymenopenaeus nereus (Faxon 1893)

Figures 9, 18B, 20-23

Haliporus nereus Faxon 1893:213 [syntypes: 1 ♀, MCZ 4645, S of Cabo Blanco, Costa Rica, 5°30′N, 86°45′W, 1,067 fm (1,952 m), 27 February 1891, *Albatross* stn 3366. 1 ♀, USNM 21177, S of Morro de Puercos, Panama, 7°06′15″N, 80°34′00″W, 695 fm (1,271 m), 23 February 1891, *Albatross* stn 3353. 2 ♀, USNM 21178, off Pen de Azuero, Panama, 6°21′N, 80°41′W, 1,793 fm (3,279 m), 7 March 1891, *Albatross* stn 3382. 1 ♂ 2 ♀, USNM 21180, NW of Is Galápagos, Ecuador, 2°34′N, 92°06′W, 1,360 fm (2,487 m), 5 April 1891, *Albatross* stn 3413. 2 ♀, MCZ 4646, NW of Punta Galera, Ecuador, 1°07′N, 80°21′W, 1,573 fm (2,877 m), 23 March 1891, *Albatross* stn 3398. 1 ♂, MCZ 4647, NW of Punta Galera, Ecuador, 1°07′N, 81°04′W, 1,740 fm (3,182 m), 24 March 1891, *Albatross* stn 3399. 2 ♀, USNM 21179, E of Is Galápagos, Ecuador, 00°36′S, 86°46′W, 1,322 fm (2,418 m), 27 March 1891, *Albatross* stn 3400. 1 ♀, Is Galápagos, Ecuador, 00°04′00″S, 90°24′30″W, 885 fm (1,619 m), 3 April 1891, *Albatross* stn 3407]. Faxon 1895: 189, pl. 48, fig. 1-1d. Bouvier 1906b:3; 1908:80. de Man 1911:7.

Hymenopenaeus nereus. Burkenroad 1936:104; 1938:60. Ramadan 1938:60. Crosnier and Forest 1973:256, fig. 83c.

Material.–Syntypes, which are the only material ever recorded; 1 ♀ collected at *Albatross* stn 3407 has not been located.

Description.–Rostrum (Figure 21) relatively short, its length about 0.3 that of carapace, reaching about midlength of second antennular article, horizontal or slightly upturned, tapering to sharp tip, and with dorsal and ventral margins straight. Rostral plus epigastric teeth 8; epigastric tooth situated at about 0.4 cl from orbital margin, first rostral (largest of all) at approximately 0.3, and base of third opposite to orbital margin. Adrostral carina low, sharp, extending from orbital margin almost to apex of rostrum; orbital margin projecting anteroventrally in narrow shelf. Postrostral carina strong to near posterior margin of carapace, followed by small tubercle. Pterygostomian spine slender and sharp, like other lateral spines on carapace; postorbital (located directly posterior to antennal), pterygostomian, and branchiostegal continuous with sharp basal carina, that continuous with branchiostegal merging with sharp hepatic carina. Cervical carina strong; sulcus extending to, but not crossing, postrostral carina, its dorsal extremity located immediately posterior to midlength of carapace; hepatic carina sharp, its accompanying sulcus deep; additional short carina lying dorsal and parallel to hepatic sulcus; posthepatic carina long, running almost to posterior margin of carapace; branchiocardiac carina also long, extending nearly to posterior margin of carapace; short sulcus extending posterodorsally from near posterior end of branchiocardiac; submarginal carina well defined, running along entire length of branchiostegite.

Eye as illustrated (Figure 18*B*).

Antennular peduncle length equivalent to about 0.4 that of carapace; prosartema broad, reaching distal margin of eye, but falling short of distal margin of first antennular article; stylocerite short, extending 0.45-0.50 of distance between its proximal extremity and mesial base of distolateral spine; latter rather long and sharp; second antennular article with transverse row of sharp spines near distal margin; antennular fla-

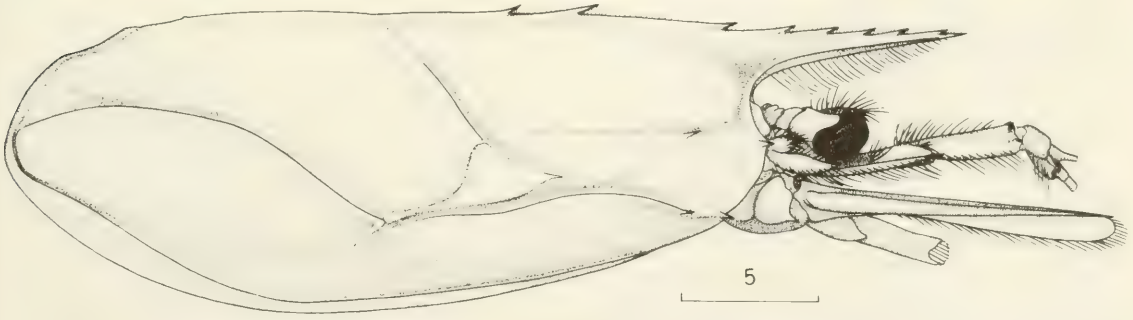

FIGURE 21.—*Hymenopenaeus nereus*, syntype ♀ 23.5 mm cl, northwest of Islas Galápagos. Cephalothorax, lateral view.

gella incomplete in specimens examined; however, in Faxon's (1895) illustration both subequal, about 1.25 times as long as carapace. Scaphocerite overreaching antennular peduncle by as much as 0.3 of its own length, with lateral rib ending in sharp, slender spine reaching, or overreaching, distal margin of lamella. Mandibular palp extending to distal 0.3 of carpocerite; proximal article about 2.6 times as long as wide. Third maxilliped reaching beyond antennular peduncle by length of dactyl and about 0.5 that of propodus; length of dactyl about 0.65 that of propodus.

First pereopod extending to distal end of carpocerite or overreaching it by 0.5 length of dactyl. Second pereopod exceeding antennular peduncle by length of propodus or by latter and 0.15 that of carpus. Third pereopod overreaching antennular peduncle by propodus and about 0.5 length of carpus. Fourth pereopod surpassing antennular peduncle by dactyl, propodus, and almost entire length of carpus. Fifth pereopod exceeding antennular peduncle by length of distal three podomeres. Pereopods increasing in length from first to fifth. First pereopod with rather inconspicuous spine on basis, and long slender spine on ischium; second pereopod with minute spine on basis. In female, coxa of third pereopod produced into large plate disposed at right angle to podomere, its anteromesial margin bearing blunt, strong tooth. Coxa of fourth pereopod produced in short, prominent plate armed with numerous strong setae. In both sexes, tooth present on anteromesial angle of coxa of fifth pereopod, tooth considerably stronger in males than in females, in latter minute and borne on rounded coxal plate.

Abdomen with middorsal keel from fourth through sixth somites, and strong longitudinal rib along lateral surface of fourth and fifth somites; posterodorsal margin of latter somites with shallow median incision; sixth somite very elongate, 2.25 times as long as high, bearing small sharp spine at posterior end of keel and pair of minute posteroventral spines. Telson with broad median sulcus, deep anteriorly, quite shallow posteriorly, and flanked by low sharp ridges; terminal portion length about 5 times basal width; lateral spines short, their length 1.5-1.6 times basal width of terminal portion of telson; mesial ramus of uropod falling short, or slightly overreaching, apex of telson; lateral ramus exceeding mesial ramus by 0.15-0.20 of its own length, and armed with acute, terminal, distolateral spine.

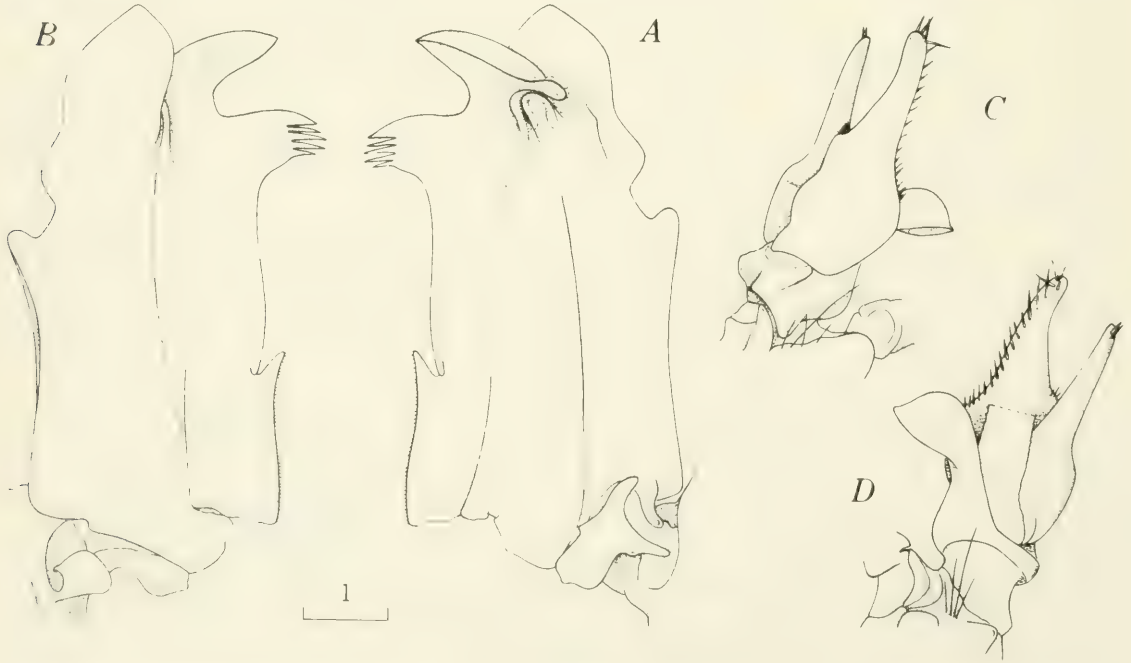

FIGURE 22.—*Hymenopenaeus nereus*, syntype ♂ 15.5 mm cl, northwest of Punta Galera, Ecuador. *A*, Petasma (partly bent laterally), dorsal view of right half. *B*, Ventrolateral view. *C*, Right appendices masculina and interna, dorsal view. *D*, Ventromesial view.

Petasma (Figure 22*A, B*) with row of cincinnuli occupying proximal 0.35 of median line; ventromedian lobule bearing two processes distally; mesial one (disposed almost at right angle to lobule) subrectangular, and armed with few long spines, distolateral one (directed at about 45 degrees to lobule) unarmed, and produced proximolaterally in small auricular process; distal flap of ventrolateral lobule acuminate, large, extending as far as lateral process, and almost straight rather than conspicuously inclined; ventral costa projecting in strong rounded prominence at base of flap.

Appendix masculina (Figure 22*C, D*) with proximal part produced into rounded lobe; distal part extremely narrow and bearing lateral row of short setae continuous with apical tuft of longer setae. Appendix interna abruptly narrowing, setting off distal part from rounded proximal part. Ventrolateral spur short, roughly semicircular in outline distally.

Thelycum (Figure 23) with median, longitudinal ridge on sternite XIV; lamella at posterior margin of sternite XIII rather flat, directed anteriorly, with distal (cephalic) margin slightly to deeply concave, and lateral margins convex basally, straight or concave distally; lamella flanked by pair of flattened, subtriangular to rounded processes directed caudally; posterior margin of sternite XII bearing paired, setose, long horns, reaching almost midlength of sternite XIII.

Maximum size.–Males: 18 mm cl; females: 27 mm cl.

Geographic and bathymetric ranges.–From south of Cabo Blanco (5°30′N, 86°45′W), Costa Rica, to northwest of Punta Galera and Islas Galápagos (00°36′S, 86°46′W), Ecuador (Figure 20). It has been found at depths between 1,271 and 3,279 m (Figure 9).

Affinities.–Hymenopenaeus nereus and *H. doris* are very similar in external morphology. However, the external genitalia allow a ready separation of these two species as well as both from the closely related *H. laevis* and *H. sewelli*. Females of *H. nereus* are unique among the four species in possessing a longitudinal ridge, instead of a large protuberance, on sternite XIV; furthermore, the median lamella of sternite XIII is directed anteriorly, its lateral margins tend to converge proximally (posteriorly), and the lamella is

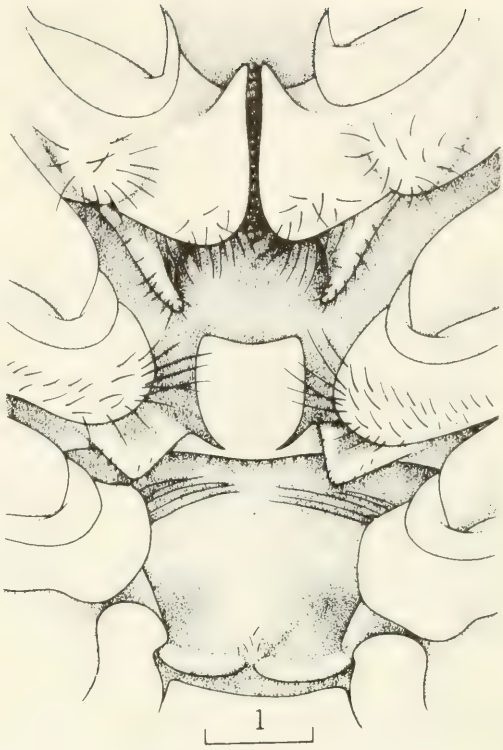

FIGURE 23.—*Hymenopenaeus nereus*, syntype ♀ 21.5 mm cl, south of Cabo Blanco, Costa Rica. Thelycum, ventral view.

flanked by a pair of processes which are flattened and directed caudally. In the other species, these processes are lacking or, if present, are directed anteroventrally. Males of *H. nereus* differ from those of *H. laevis* in that the petasma of the latter bears two, occasionally three, small, triangular projections on the distomesial margin of the ventromedian lobule instead of a single, subrectangular process bearing spines distally. Moreover, the lateral process is small and extends transversely rather than being directed distomesially, and the distal part of the ventrolateral lobule is broadly semicircular and strongly inclined toward the ventromedian lobule.

Haliporoides Stebbing 1914

Peneopsis. Faxon 1893:212; 1895:185.

Faxonia Bouvier 1905a:981 [part, excluding type-species, *Penaeopsis ocularis* Faxon 1895 = *Pleoticus robustus* (Smith 1885)].

Haliporus. Bouvier 1906b:1 [part]; 1908:78 [part]. de Man 1911:31 [part]. Calman 1925:9.

Haliporoides Stebbing 1914:20 [type-species, by monotypy, *Haliporoides triarthrus* Stebbing 1914. Gender, masculine]. Calman 1925:9.
Hymenopenaeus. Burkenroad 1936:102 [part].
Parahaliporus Kubo 1949:207.
Hymenopenaeus (Haliporoides). Barnard 1950: 619.

Diagnosis.–Body moderately robust, carapace elongate, integument firm. Rostrum relatively long, extending at least to, often beyond, second antennular article, ventral margin straight or concave; armed with dorsal and, frequently, with ventral teeth; epigastric tooth separated from rostral teeth by interval noticeably longer than spaces between latter. Orbital and branchiostegal spines absent; postorbital, antennal, pterygostomian, hepatic, and suprahepatic spines present. Cervical sulcus deep, long, extending to, but not across, middorsum of carapace; hepatic sulcus long, turning anteroventrally from almost horizontal posterior part and reaching base of pterygostomian spine; orbital-antennal and branchiocardiac carinae and sulci well marked; submarginal carina sharp. Abdomen carinate dorsally at least along three posterior somites. Telson with pair of fixed, lateral spines. Prosartema moderately long, broad, and flexible. Antennular flagella similar, subcylindrical and long, not less than 3 times carapace length. Mandibular palp three jointed (occasionally two jointed in *H. triarthrus*, Ivanov and Hassan 1976), proximal article short and narrow, intermediate one larger, scalene-triangular in shape, and distal article considerably shorter and narrower than preceding one and tapering to blunt apex. First maxilla with unsegmented palp, gently narrowing to rounded apex. Fourth and fifth pereopods relatively stout proximally, fifth not much longer than fourth. First pereopod with or without spine on basis. Exopods (quite small) on all maxillipeds and pereopods. Lateral ramus of uropod armed with subterminal, distolateral spine. In males, petasma with distal part of ventral costa fused to flexible flap of ventrolateral lobule; distal portion of rib of dorsolateral lobule not elevated above, but at level of adjacent area, and not projecting beyond distal margin; ventromedian lobule lacking paired processes distally; endopod of second pleopod bearing appendices masculina and interna, its basal sclerite produced into very short, toothlike, ventrolateral spur. Thelycum of open type. Pleurobranchia present on somites IX to XIV; single, rather conspicuous arthrobranchia on somite VII, and anterior and posterior arthrobranchiae on somites VIII to XIII. Podobranchia present on second maxilliped, and epipod on second maxilliped (and on first if proximal exite of coxa considered an epipod) through fourth pereopod.

List of species.–Eastern Pacific: *Haliporoides diomedeae* (Faxon 1893). Indo-West Pacific: *Haliporoides sibogae* (de Man 1907); *Haliporoides triarthrus* Stebbing 1914.

Affinities.–The members of *Haliporoides* can be distinguished readily from those belonging to other related genera by the following features: the epigastric tooth is separated from the series of rostral teeth by an interval conspicuously longer than the spaces between the latter; the presence of a suprahepatic spine and an orbitoantennal sulcus which, although shallow, is clearly distinct; the spine of the lateral ramus of the uropod which is subterminal. Also, the arthrobranchia on somite VII is well developed instead of being rudimentary and, in males, the basal sclerite of the second pleopod is produced into a very short, toothlike, rather than foliaceous, ventrolateral spur.

In addition to the characters cited above, *Haliporoides*, in contrast to *Hymenopenaeus*, possesses a thick, rigid integument, and lacks a branchiostegal spine and a posthepatic carina; it also possesses a petasma in which the ventromedian lobule is not produced distally into conspicuous processes, and the rib of the dorsolateral lobule is flush with the surrounding area. Finally, *Haliporoides* may be separated from *Pleoticus*–which it resembles in its general mien and in the shape of the rostrum—not only by the characters cited, but also by possessing a sharp branchiocardiac carina and deep branchiocardiac sulcus as well as by the petasma, in which the ventral costa is fused to the terminal part of the ventrolateral lobule. The above clearly indicates that *Haliporoides* is the most distinct of the genera treated here, except perhaps for *Mesopenaeus*.

Haliporoides diomedeae (Faxon 1893)

Figures 9, 20, 24-28

Peneopsis diomedeae Faxon 1893:212 [syntypes: 3 ♀, USNM 21175, off Golfo de Panamá, 7°31′30″N, 79°14′00″W, 458 fm (838 m), 8 March

1891, *Albatross* stn 3384. 1 ♂ 1 ♀, USNM 21176, SW of Golfo de Panamá, 7°30′36″N, 78°39′00″W, 730 fm (1,335 m), 11 March 1891, *Albatross* stn 3395. 2 ♂ 1 ♀, MCZ 4644, SE of Golfo de Panamá, 7°21′N, 79°35′W, 511 fm (935 m), 10 March 1891, *Albatross* stn 3394. 3 ♀, off Punta Mala, Panama, 7°15′N, 79°36′W, 1,020 fm (1,866 m), 10 March 1891, *Albatross* stn 3393. 2 ♀, off Punta Mariato, Panama, 7°06′15″N, 80°34′00″W, 695 fm (1,271 m), 23 February 1891, *Albatross* stn 3353. 1 ♂, USNM 21174, S of Península de Azuero, 6°30′N, 81°44′W, 555 fm (1,015 m), 24 February 1891, *Albatross* stn 3358]. Faxon 1895:185, pl. G.

Faxonia diomedeae. Bouvier 1905a:981.

Haliporus diomedeus. Bouvier 1906b:4; 1908:80.

Haliporus diomedeae. de Man 1911:7.

Hymenopenaeus diomedeae. Burkenroad 1936: 104. Hancock and Henríquez 1968:445. Idyll 1969:641. Chirichigno Fonseca 1970:13, fig. 18. del Solar C. et al. 1970:18. Arana Espina and Cristi V. 1971:25. Illanes B. and Zúñiga C. 1972: 3, pl. 1-2.

Hymenopenaeus diomedaea. Bahamonde 1963:3 (unnumbered).

Vernacular names; gamba roja (Peru); gamba, camarón de mar, camarón de profundidad (Chile).

Material

PANAMA—2 ♀, MCIP, 32 km SE of Punta Mala, Península de Azuero, 823-1,006 m, 1973, *Canopus*. 3 ♀ syntypes, USNM 21175, off Golfo de Panamá, 458 fm (838 m), 8 March 1891, *Albatross* stn 3384. 1 ♂ 1 ♀ syntypes, USNM 21176, SW of Golfo de Panamá, 730 fm (1,335 m), 11 March 1891, *Albatross* stn 3395. 2 ♂ 1 ♀ syntypes, MCZ 4644, SE of Golfo de Panamá, 511 fm (935 m), 10 March 1891, *Albatross* stn 3394. 1 ♂ syntype, USNM 21174, S of Península de Azuero, 555 fm (1,015 m), 24 February 1891, *Albatross* stn 3358.

PERU—1 ♀, USNM, off Casitas, Tumbes, 550 m, 16 December 1968, *Kaiyo Maru*. 58 ♂ 56 ♀, USNM, W of I Macabí, 607-735 m, 5 September 1966, *Anton Bruun* stn 754.

CHILE—4 ♀, USNM, off Paposo, Antofagasta, 950 m, 16 August 1966, *Anton Bruun* stn 714. 8 ♂ 13 ♀, USNM, off Bahía Pichidangui, Coquimbo, 960 m, 12 August 1966, *Anton Bruun* stn 703. 1 ♂ 1 ♀, USNM, Valparaíso, 10 February 1956, John Manning. 14 ♂ 17 ♀, USNM, off Punta Topocalma, Colchagua, 750-730 m, 5 August 1966, *Anton Bruun* stn 687.

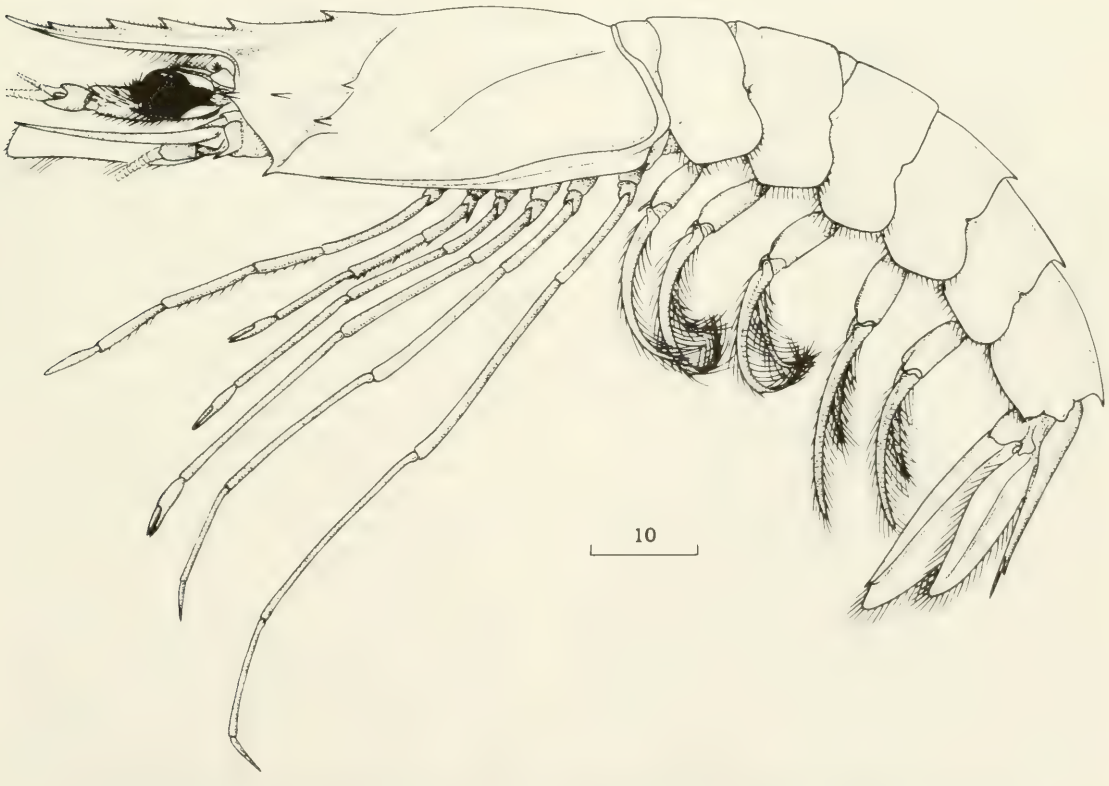

FIGURE 24.—*Haliporoides diomedeae*, ♀ 37.5 mm cl, off Bahía Pichidangui, Coquimbo, Chile. Lateral view.

Description.–Body rather robust (Figure 24), integument firm and glabrous. Rostrum straight or gently sinuous with upturned tip, moderately long, at most slightly overreaching antennular peduncle, its length 0.45-0.60 that of carapace. Rostral plus epigastric teeth 3-6 (mode 5; N = 100); epigastric tooth situated at about 0.3 length of carapace from orbital margin, first rostral at level of, or immediately posterior to, orbital margin. Adrostral carina strong, extending from orbital margin almost to apex of rostrum; postrostral carina very strong to near posterior margin of carapace, there merging with inconspicuous dorsal tubercle. Antennal, pterygostomian, postorbital, and hepatic spines long, slender, and sharp; both antennal and postorbital spines (latter situated directly posterior to antennal) continuous with short, blunt, basal carina; basally broad suprahepatic spine (occasionally accompanied by smaller dorsal one) present, giving rise to deep notch dorsal to hepatic spine; orbitoantennal sulcus shallow, but clearly distinct; cervical carina sharp, cervical sulcus deep, extending to, but not crossing, postrostral carina, its dorsal extremity located almost 0.45 length of carapace from orbital margin; hepatic sulcus deep, hepatic carina sharp anteriorly and turning anteroventrally to base of pterygostomian spine; both hepatic carina and sulcus almost indistinct posteriorly, to anteroventral end of branchiocardiac sulcus. Branchiocardiac carina long, sinuous, and sharp, accompanying sulcus deep and broad; submarginal carina long, extending from base of pterygostomian spine to posterior margin of carapace.

Eye (Figure 25) with basal article produced distomesially into pubescent, relatively short scale; ocular peduncle short, bearing rather small mesial tubercle; cornea subreniform, greatest diameter about 2 times that of base of ocular peduncle, strongly slanting posterolaterally.

Antennular peduncle length equivalent to about 0.5 that of carapace; prosartema broad and short, extending only to distomesial extremity of ocular peduncle; stylocerite extending about 0.6 of distance between its proximal extremity and mesial base of distolateral spine; latter moderately long, slender, and sharp. Antennular flagella long, although incomplete in all specimens examined, in shrimp 32.5 mm cl, broken dorsal flagellum 118 mm long, thus 3.65 times as long as carapace. Scaphocerite overreaching antennular peduncle by about 0.2 of its own length;

FIGURE 25.—*Haliporoides diomedeae*, ♀ 44.5 mm cl, off Punta Topocalma, Colchagua, Chile. Eye.

lateral rib ending in rather slender spine, falling short of distal margin of lamella. Antennal flagellum broken in specimens examined, according to Illanes and Zúñiga (1972) "longer than total length of body."

Mandibular palp (Figure 26*A*) extending as far as basal 0.4 length of carpocerite; proximal article scalene-triangular, about 2.65 times as long as wide; distal article considerably shorter and narrower than proximal, and tapering to blunt tip. First and second maxillae as illustrated (Figure 26*B, C*); somite VII bearing single conspicuous arthrobranchia at base of first maxilliped (Figure 26*De-e*[1]). Third maxilliped reaching beyond antennular peduncle by tip or by length of dactyl in males and by as much as dactyl and 0.5 length of propodus in females; dactyl with acute tip in females, clublike in males, its length 0.90-0.95 that of propodus.

First pereopod reaching between base and distal end of carpocerite in males, and almost to distal end of carpocerite or overreaching it by as much as length of dactyl in females. Second pereopod extending, at most, to midlength of second antennular article in males, and as far as distal end of third article in females. Third pereopod reaching distal end of third antennular article or overreaching it by not more than length of dactyl in males, and by entire propodus plus 0.15 length of carpus in large females. Fourth pereopod exceeding antennular peduncle by, at most, length of dactyl in males, and by dactyl or by entire propodus in females. Fifth pereopod overreaching antennular peduncle by as much as length of dactyl and 0.8 that of propodus in males, and by distal two podomeres plus 0.15-0.25 length

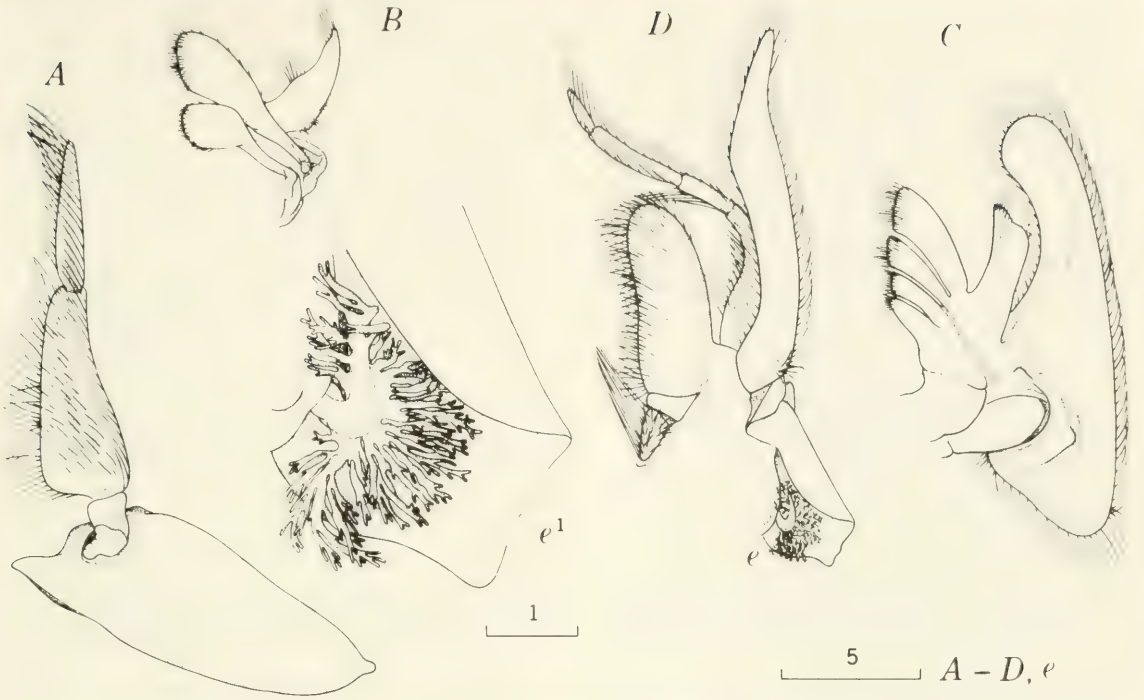

FIGURE 26.—*Haliporoides diomedeae*, ♀ 45.5 mm cl, Valparaíso, Chile. *A*, Mandible. *B*, First maxilla. *C*, Second maxilla. *D*, First maxilliped. *e*, Arthrobranchia. e^1, Enlargement of *e* (all from left side).

of carpus in females. Pereopods increasing in length from first to fifth; third and fourth extending distally for about same distance. First pereopod with spine on basis and ischium, and one movable distal spine and one or two fixed proximal ones on merus; basis of second pereopod lacking spine. In females, coxal plate of third pereopod directed and broadening mesially, strongly convex posteriorly. In both sexes, anteromesial spine present on coxae of third through fifth pereopods; in females, spine on third long, slender, and situated anterodorsally to coxal plate, and spines on fourth and fifth small and sharp; in males, spines on third and fourth pereopods small and sharp, but spine on fifth large, flattened, curved laterally.

Abdomen with middorsal keel from fourth through sixth somites and strong, sharp spine at posterior end of keel on each; sixth somite short, about 1.25 times as long as high, bearing posteroventral spines. Telson with broad median sulcus deep anteriorly, shallower posteriorly, ending at level of base of lateral spines, and flanked by well-defined ridges; terminal portion length 4-5 times basal width, spines short, 1.0-1.65 times basal width of terminal portion. Mesial ramus of uropod reaching apex of telson or overreaching it by about 0.15 of its own length; lateral ramus, in turn, overreaching mesial by almost 0.2 of its own length, armed with rather strong, subterminal, distolateral spine. Third through fifth pleopods in males bearing strong dorsomesial ridge, that of third bearing distally strong subrectangular tooth with minute tooth at its base; ridge on fourth ending in also large, subtriangular tooth; last three pleopods in females with barely marked dorsomesial ridge.

Petasma (Figure 27*A*, *B*) with row of cincinnuli occupying only proximal 0.3 of median line; terminal part of ventromedian lobule abruptly broadening distally with terminal margin serrate laterally; rib of dorsolateral lobule broad proximally, its distal extremity reaching, but not overreaching, margin of adjacent membranous portion; distal part of ventrolateral lobule free, forming roughly subelliptical flap diverging from ventromedian lobule; ventral costa broad proximally, tapering along margin of flap.

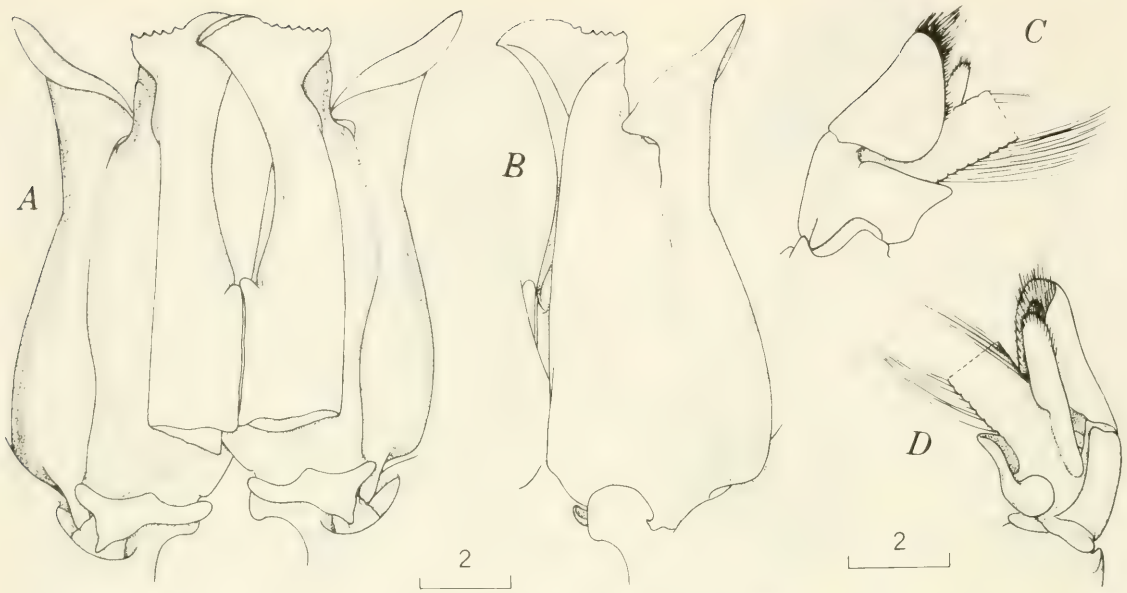

FIGURE 27.—*Haliporoides diomedeae*, ♂ 34.5 mm cl, off Bahía Pichidangui, Coquimbo, Chile. *A*, Petasma, dorsal view (partly bent laterally). *B*, Ventral view of left half. *C*, Right appendices masculina and interna, dorsal view. *D*, Ventromesial view.

Appendix masculina (Figure 27*C*, *D*) short, length about 1.5 times maximum width, produced laterally into broad semicircular lobe, ventrally excavated and bearing patch of long setae along entire distal margin. Appendix interna falling short of distal margin of appendix masculina, and armed with thickly set setae along entire distal margin; distolateral spur very short and obtuse.

Thelycum (Figure 28) with no ridge or protuberance on sternite XIV, latter smoothly convex or low subconical, often bearing minute central tubercle; posterior part of sternite XIII armed with strong median, acute to blunt subconical protuberance directed anteriorly and studded with numerous setae on anterior half; posterior margin of sternite XII lacking horns.

Color.–Overall pink with red and orange patches and bands, both longitudinal and transverse. For detailed account of coloration see Illanes B. and Zúñiga C. (1972).

Maximum size.–Males: 50 mm cl; females: 57 mm cl (in material examined by me).

Geographic and bathymetric ranges.–Off Península de Azuero, Panama (Figure 20) to Talcahuano, Chile (36°40′S), in depths between 240 (Illanes B. and Zúñiga C. 1972) and 1,866 m (Figure 9). Information on the geographic and bathymetric distributions of this species, as well as of its other two congeners in the American Pacific, is extremely meager.

Affinities.–*Haliporoides diomedeae* is the only member of the genus occurring in American waters and may thus be readily distinguished from the other solenocerids in the region by generic characters. Its two congeners, the Indo-West Pacific *H. sibogae* and *H. triarthrus*, differ from it in possessing an arcuate, ventrally toothed rostrum, and in lacking meral spines on the first pair of pereopods, as well as in petasmal and thelycal features. In both of them, the ventromedian lobule of the petasma is neither expanded distally nor serrate along its terminal margin, and the thelycum exhibits a midridge on sternite XIII instead of a subconical, median protuberance.

Remarks.–Studies of this species are extremely few, and almost entirely restricted to its external morphology. The most recent contribution is one by Illanes B. and Zúñiga C. (1972), who presented many fine observations on numerous features. Previously, Arana Espina and Cristi V. (1971) had determined the relations between the following parameters: carapace length, total length,

whole weight, and abdominal weight (cl/tl, cl/ww, cl/aw, tl/ww, tl/aw). They found statistically significant differences between males and females in all relations with the exception of carapace length/total length.

Economic importance.–At present this species is not taken commercially. However, dense concentrations have been located in various areas within its range. Off the west coast of America three deepwater shrimps—*Solenocera agassizii* Faxon 1893; *Solenocera florea* Burkenroad 1938, and *Heterocarpus reedi* Bahamonde 1955—are utilized; consequently, it is to be expected that *H. diomedeae,* a species larger than those mentioned above, eventually will be exploited.

Pleoticus Bate 1888

Philonicus Bate 1888:273 [part, excluding *Philonicus lucasii* (Bate 1881) = *Hadropenaeus lucasii,* and *Philonicus pectinatus* Bate 1888 = *Solenocera pectinata*]. [Type-species, by subsequent designation of Fowler 1912:543, *Philonicus mülleri* Bate 1888]. Preoccupied by *Philonicus* Loew 1849:144 (Diptera).

Pleoticus Bate 1888:xii [part]. [Replacement name for *Philonicus* Bate. Type-species, *Philonicus mülleri* Bate 1888. Gender, masculine].

Faxonia Bouvier 1905a:981 [part, excluding *Faxonia diomedeae* (Faxon 1893)]. [Type-species, by subsequent designation of Fowler 1912:543, *Penaeopsis ocularis* Faxon 1895 = *Pleoticus robustus* (Smith 1885)].

Parartemesia Bouvier 1905b:747 [part, excluding *Parartemesia tropicalis* Bouvier 1905b = *Mesopenaeus tropicalis* (Bouvier 1905b)]. [Type-species, by subsequent designation of Fowler 1912:543, *Parartemesia carinata* Bouvier 1905b = *Pleoticus muelleri* (Bate 1888)].

Haliporus. Bouvier 1906b:1 [part]; 1908:78 [part]. A. Milne Edwards and Bouvier 1909:206 [part]. de Man 1911:31 [part]. Fowler 1912:542 [part].

Hymenopenaeus. Smith 1885:179 [part]. Burkenroad 1936:102 [part]. Kubo 1949:212 [part]. Roberts and Pequegnat 1970:29 [part].

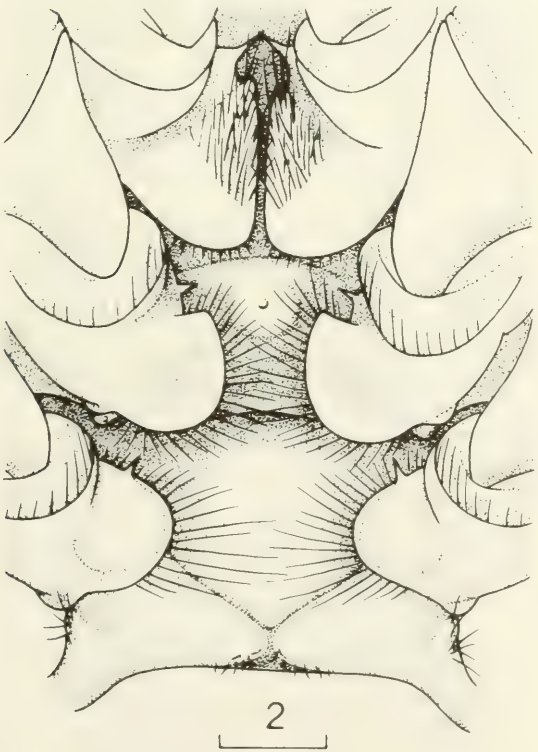

FIGURE 28.—*Haliporoides diomedeae,* ♀ 44.5 mm cl, off Punta Topocalma, Colchagua, Chile. Thelycum, ventral view.

Diagnosis.–Body robust, carapace elongate, integument thick, firm. Rostrum moderately long, reaching midlength of second antennular article or slightly overreaching peduncle; ventral margin straight to concave; armed only with dorsal teeth; epigastric tooth and first rostral separated by interval equal to, or only slightly greater than, that between first and second rostral teeth. Orbital, postorbital, antennal, and hepatic spines present; pterygostomian spine absent; branchiostegal spine present or absent. Cervical sulcus deep, long, extending to, but not across, middorsum of carapace; hepatic sulcus well marked; posthepatic and branchiocardiac carina lacking; branchiocardiac sulcus usually absent; submarginal carina sharp; posthepatic carina absent. Abdomen carinate dorsally at least along posterior three somites. Telson with pair of conspicuous, fixed lateral spines. Prosartema long or moderately long, flexible. Antennular flagella similar, subcylindrical, and longer than carapace. Mandibular palp two jointed, articles broad, distal one as long, or almost as long, as basal, tapering to blunt apex. First maxilla with unsegmented palp, gently narrowing to rounded apex. Fourth and fifth pereopods rather stout proximally, fifth moderately longer than fourth. First pereopod with spine on basis and ischium. Exopods on all maxillipeds and pereopods. Lateral ramus of

uropod armed with terminal, distolateral spine. In males, petasma with ventral costa free from distally flexible terminal part of ventrolateral lobule; ventromedian lobule not expanded distally. Endopod of second pleopod bearing appendices masculina and interna, and with basal sclerite produced distally into elongate ventrolateral spur. Thelycum of open type, lacking enclosed seminal receptacle. Pleurobranchia present on somites IX to XIV; one or two rudimentary arthrobranchiae on somite VII; and anterior and posterior arthrobranchiae on somites VIII to XIII. Podobranchia present on second maxilliped, and epipod on second maxilliped (and on first if proximal exite of coxa considered an epipod) through fourth pereopod.

List of species.–Western Atlantic: *Pleoticus robustus* (Smith 1885); *Pleoticus muelleri* (Bate 1888). Red Sea: *Pleoticus steindachneri* (Balss 1914).

Affinities.–The members of *Pleoticus* resemble those of *Hymenopenaeus* and *Haliporoides* in the character of the rostrum and general form of the carapace; however, in *Pleoticus* the epigastric tooth is separated from the first rostral by an interval which is equal to, or only slightly greater than, that between the first and second rostral teeth; an orbital spine is present as it only is in the more distantly related *Mesopenaeus;* the branchiocardiac carina is absent; and the branchiocardiac sulcus is usually absent. Furthermore, the mandibular palp is two jointed unlike the usually three jointed one of *Haliporoides* but like that of *Hymenopenaeus;* however, in contrast to the palp of the latter, that of *Pleoticus* is broad and its distal article is as long as, or longer than, the basal. Finally, in the petasma of *Pleoticus* the distal extremity of the ventral costa is free from the ventrolateral lobule instead of being fused to it.

Pleoticus agrees with *Hadropenaeus* in the arrangement of the epigastric and rostral series of teeth, the lack of branchiocardiac and posthepatic carinae, the absence of pterygostomian spines, as well as in having the distal extremity of the ventral costa of the petasma free from the adjacent part of the ventrolateral lobule. The considerably more elongate carapace, the low and longer rostrum, and the presence of strong submarginal carina, and orbital spine separate the former from the latter.

The similarities cited above indicate that *Pleoticus* occupies a position somewhat intermediate between the more primitive *Hymenopenaeus* and *Haliporoides,* on one hand, and *Hadropenaeus* on the other.

The genus *Pleoticus* is less homogeneous than the other genera treated here. In *P. robustus* and *P. muelleri* the branchiocardiac sulcus is abent or indistinct whereas in *P. steindachneri* it is distinctly marked; the branchiostegal spine, while present in *P. robustus* and *P. muelleri,* is lacking in *P. steindachneri.* Whereas in the petasma of *P. robustus* and *P. steindachneri* the row of cincinnuli occupies almost the entire median line, and the ventromedian lobule is distally membranous and entire, in that of *P. muelleri* the row of cincinnuli is limited to the proximal 0.4 of the median line, and the ventromedian lobule is heavily sclerotized distally and bears strong projections. In spite of these differences, it seems to me that the many features shared by these species justify their being grouped within a single genus. I have not examined specimens of *P. steindachneri,* but the descriptions and illustrations of Balss (1914, 1915) indicate that this shrimp is more closely related to *P. robustus* and *P. muelleri* than to members of other genera.

Key to the Species of *Pleoticus* in the western Atlantic

1. Body entirely pubescent. Prosartema not overreaching distal margin of first antennular article. Branchiostegal spine present. Females with paired, triangular projections near anterior margin of sternite XIV, and strong median ridge on sternite XIII. Males with petasma cincinnulate along entire median line, its ventromedian lobule entire distally ..... *P. robustus*

   Body almost entirely polished. Prosartema considerably overreaching distal margin of first antennular article. Branchiostegal spine absent. Females lacking triangular projections on sternite XIV, bearing strong, median projection on sternite XIII. Males with petasma cincinnulate along proximal 0.4 of median line, its ventromedian lobule produced in two projections .... *P. muelleri*

Pleoticus robustus (Smith 1885)

Figures 9, 29-36

Hymenopenaeus robustus Smith 1885:180 [syntypes: 2 ♂ 7 ♀, USNM 6907; 2 ♂ 5 ♀ (1 ♀ in original lot = *Penaeopsis serrata* Bate 1881), USNM 6908; type-locality: 11°43′00″N, 69°09′30″W, 208 fm (380 m), S of Curaçao, *Albatross* stn 2125]. Burkenroad 1936:118. Anderson and Lindner 1945:288. U.S. Fish and Wildlife Service 1948:2. Springer 1951a:80; 1951b: 6. Springer and Bullis 1952:11. Popovici and Angelescu 1954:509. Springer and Bullis 1954: 3. Voss 1955:9, fig. 6. Bullis 1956:1 [not Fig. 1 = *Aristeus antillensis* A. Milne Edwards and Bouvier 1909]. Springer and Bullis 1956:8. Clifford 1956:438. Guest 1956:7. Lindner 1957:87. Anderson 1958:1, fig. 6. U.S. Fish and Wildlife Service 1958:1, fig. I-6. Bullis and Thompson 1959a:35; 1959b:1. Hutton et al. 1959:7. Eldred and Hutton 1960:91, fig. 12. Cummins and Rivers 1962:19. Bullis and Cummins 1963:9. Davant 1963:21, fig. 19-20. Boschi 1964:38. Hutton 1964:439. Bullis and Thompson 1965:5. Holthuis and Rosa 1965:1. Pericchi López 1965: 24. Joyce and Eldred 1966:24. Kutkuhn 1966: 21. Christmas and Gunter 1967:1442. Thompson 1967:1454. Idyll 1969:638. Klima 1969:1. Roe 1969:161, fig. 1. Anderson and Bullis 1970: 112. Pérez Farfante 1970:13, fig. 3F-H. Roberts and Pequegnat 1970:30, fig. 3-1B-C. Anderson and Lindner 1971:313, fig. 1-7. García Pinto 1971:5. Pequegnat and Roberts 1971:8. García del Barco 1972:172.

Peneopsis ocularis Faxon 1895:187.

Faxonia ocularis. Bouvier 1905a:981.

Haliporus robustus. Bouvier 1906b:4; 1908:8. A. Milne Edwards and Bouvier 1909:210, fig. 29-37, pl. 1, fig. 14-15, pl. 2, fig. 1-7. de Man 1911:7. Lenz and Strunck 1914:303. Burkenroad 1934:69.

Parapenaeus paradoxus Boone 1927:79 [part].

Hymenopeneus robustus. Burkenroad 1963a:173.

Royal red shrimp. Bates 1957:9, figures. Bullis and Rathjen 1959:1. Anonymous 1977:2.

Vernacular names: royal red shrimp (United States), camarón rojo gigante (Mexico), camarón real rojo (Cuba), langostino rojo (Venezuela).

Material

UNITED STATES—Massachusetts: 2 ♂ 2 ♀, USNM, S of Martha's Vineyard, 320 m, 28 January 1960, *Delaware* stn 39. 1 ♀, USNM, off Georges Bank, 20 July 1955, *Delaware*. North Carolina: 1 ♂ 1 ♀, USNM, NE of Cape Lookout, 348-384 m, 13 November 1956, *Combat* stn 171. 6 ♀, USNM, off Cape Lookout, 366 m, 22 June 1957, *Combat*

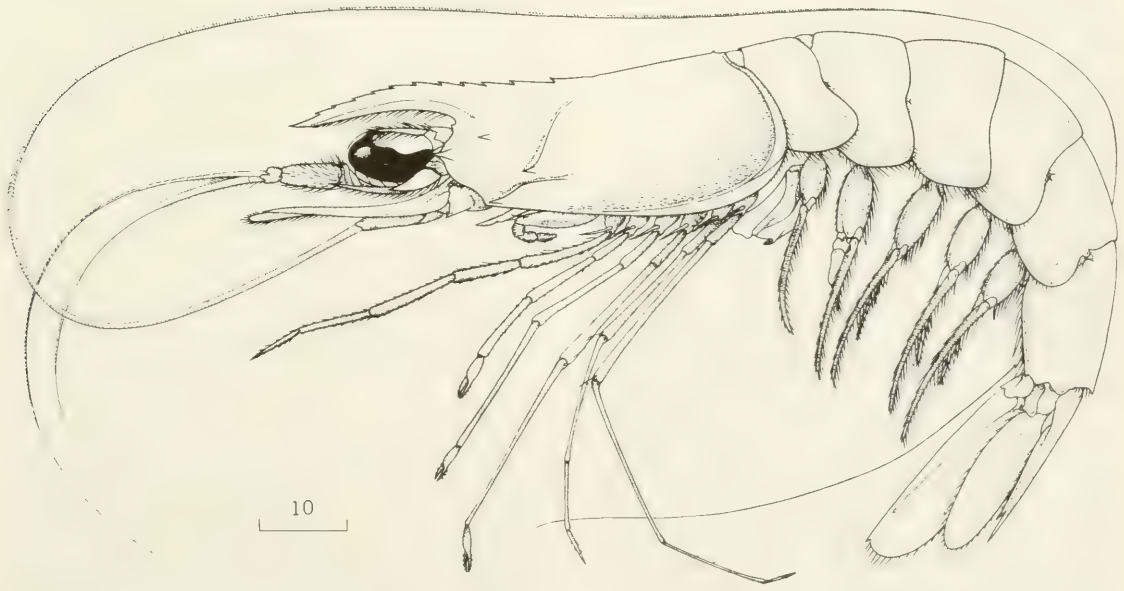

FIGURE 29.—*Pleoticus robustus*, ♂ 31 mm cl, east of Península Valiente, Panama. Lateral view.

stn 410. 5 ♂ 5 ♀, USNM, SE of Cape Fear, 402 m, 29 January 1972, *Oregon II* stn 11746. South Carolina: 1 ♂ 1 ♀, USNM, off Port Royal Sound, 366 m, 23 January 1972, *Oregon II* stn 11734. Florida: 3 ♂, USNM, off St Augustine, 384-393 m, 9 February 1965, *Oregon* stn 5231. 1 ♂ 3 ♀, USNM, off St Augustine, 344-338 m, 1 May 1956, *Pelican* stn 41. 3 ♀, USNM, off St Augustine, 316-329 m, 2 May 1956, *Pelican* stn 46. 1 ♂ 22 ♀, USNM, off St Augustine, 324-333 m, 3 February 1962, *Silver Bay* stn 3725. 28 ♂ 30 ♀, USNM, off Flagler Beach, 384 m, 16 November 1964, *Oregon* stn 5107. 1 ♂ 2 ♀, USNM, off Coronada Beach, 348 m, 10 February 1965, *Oregon* stn 5241. 9 ♂ 6 ♀, USNM, off Oak Hill, 402-430 m, 11 February 1965, *Oregon* stn 5247. 4 ♀, USNM, off Cape Kennedy, 338 m, 27 January 1962, *Silver Bay* stn 3714. 5 ♂ 6 ♀, USNM, off Cocoa Beach, 329 m, 11 March 1956, *Pelican* stn 13. 11 ♂ 15 ♀, RMNH, E of Hutchinsons I, 324 m, 16 July 1965, *Gerda* stn 654. 11 ♂ 13 ♀, UMML, off St Lucie Inlet, 366-375 m, 21 May 1968, *Gerda* stn 998. 15 ♂ 14 ♀, USNM, SE of St Lucie Inlet, 287-262 m, 16 July 1965, *Gerda* stn 655. 2 ♂, USNM, E of Carysfort Reef, 549 m, 23 July 1957, *Combat* stn 444. 1 ♂ 1 ♀, USNM, off Islamorada, 457-476 m, 18 July 1955, *Oregon* stn 1351. 3 ♂ 2 ♀, USNM, off Double Headed Shot Cays, 558-514 m, 29 August 1967, *Gerda* stn 861. 1 ♀, UMML, S of Marquesas Keys, 512 m, 2 February 1968, *Gerda* stn 970. 9 ♀, USNM, SW of Marquesas Keys, 402-267 m, 2 February 1968, *Gerda* stn 969. 6 ♂ 4 ♀, USNM, SW of Marquesas Keys, 437-320 m, 2 February 1968, *Gerda* stn 968. 1 ♀, UMML, S of Dry Tortugas, 622 m, 28 April 1969, *Gerda* stn 1099. 2 ♂ 3 ♀, UMML, S of Dry Tortugas, 459-494 m, 28 April 1969, *Gerda* stn 1098. 26 ♂ 27 ♀, USNM, SW of Dry Tortugas, 348 m, 13 April 1954, *Oregon* stn 1005. 5 ♂ 8 ♀, USNM, SW of Dry Tortugas, 402 m, 15 June 1956, *Oregon* stn 1539. 1 ♂, USNM, NW of Dry Tortugas, 311-366 m, 7 July 1955, *Oregon* stn 1321. 2 ♂ 2 ♀, USNM, S of St George I, 366 m, 21 August 1970, *Oregon II* stn 11180. 2 ♂ 2 ♀, USNM, S of Santa Rosa I, 439 m, 28 August 1970, *Oregon II* stn 11189. 1 ♀, USNM, S of Santa Rosa I, 527 m, 4 February 1970, *Oregon II* stn 10899. 9 ♂ 6 ♀, USNM, off Gulf Beach, 576-622 m, 28 April 1951, *Oregon* stn 319. Alabama (all from off Mobile Bay): 4 ♀, USNM, 549 m, 10 August 1970, *Oregon II* stn 11137. 1 ♀, USNM, 594 m, 10 August 1970, *Oregon II* stn 11139. 2 ♂ 2 ♀, USNM, 433 m, 22 June 1969, *Oregon II* stn 10640. 1 ♂ 4 ♀, USNM, 366 m, 18 December 1962, *Oregon* stn 4151. 8 ♀ juv, YPM, 219-238 m, 24 March 1935, *Atlantis* stn 2377. 3 ♀, USNM, 512 m, 10 July 1952, *Oregon* stn 597. Louisiana: 1 ♂, AMNH, E of Mississippi Delta, 384 m, 11 February 1885, *Albatross* stn 2377. 1 ♂, USNM, E of Mississippi Delta, 357 m, 1 September 1970, *Oregon II* stn 11202. 4 ♀, USNM, E of Mississippi Delta, 549 m, 23 October 1962, *Oregon* stn 4005. 14 ♂ 9 ♀, USNM, E of Mississippi Delta, 357 m, 23 September 1950, *Oregon* stn 126. 7 ♂ 10 ♀, USNM, E of Mississippi Delta, 402 m, 22 April 1951, *Oregon* stn 307. 3 ♂ 17 ♀, USNM, E of Mississippi Delta, 402 m, 25 August 1962, *Oregon* stn 3733. 1 ♀, YPM, E of Mississippi Delta, 302 m, 26 March 1935, *Atlantis* stn 2381. 3 ♂, USNM, off Atchafalaya Bay, 402 m, 11 November 1951, *Oregon* stn 501. Texas: 2 ♂ 3 ♀, USNM, SSE of Galveston, 366 m, 18 November 1951, *Oregon* stn 503. 3 ♂ 4 ♀ 2 juv, USNM, E of St Joseph I, 503 m, 6 May 1956, *Oregon* stn 1506. 1 ♂, USNM, off Corpus Christi, 640-732 m, 16 April 1952, *Oregon* stn 543. 1 ♂ 2 ♀, USNM, off Padre I, 549 m, 23 January 1964, *Oregon* stn 4637. 1 ♂ juv, USNM, off Port Isabel, 640 m, 6 August 1969, *Western Gulf* stn 38. 1 ♀, USNM, off Brownsville, 457 m, 6 August 1969, *Western Gulf* stn 39.

MEXICO—Tamaulipas: 1 ♂ 1 ♀, USNM, off Las Lavaderos, 558 m, 2 June 1970, *Oregon II* stn 10953. 2 ♀, USNM, off Las Lavaderos, 677 m, 2 June 1970, *Oregon II* stn 10954. Veracruz: 2 ♂ 2 ♀, USNM, N of Punta Roca Partida, 357 m, 5 June 1970, *Oregon II* stn 10959. 1 ♂ 1 ♀, USNM, NE of Punta Roca Partida, 613 m, 5 June 1970, *Oregon II* stn 10960. Tabasco: 1 ♀, USNM, NW of Laguna del Carmen, 430 m, 6 June 1970, *Oregon II* stn 10963. 1 ♀, USNM, N of Punta Frontera, 613 m, 9 June 1970, *Oregon II* stn 10984.

HAITI—14 ♂ 7 ♀, USNM, off Cape-Haitien, 640 m, 12 February 1963, *Silver Bay* stn 5142.

DOMINICAN REPUBLIC—1 ♂ 1 ♀, USNM, E of Puerto Plata, 732-640 m, 15 October 1963, *Silver Bay* stn 5168.

LESSER ANTILLES—4 ♀, USNM, off Dog I, 628 m, 6 December 1969, *Oregon II* stn 10835. 2 ♀, USNM, off Dog I, 688 m, 6 December 1969, *Oregon II* stn 10834. 7 ♂ 6 ♀, USNM, NE of Saba I, 649-668 m, 18 May 1967, *Oregon* stn 6696. 4 ♂ 5 ♀, USNM, E of Sint Eustatius, 642 m, 8 December 1969, *Oregon II* stn 10840. 2 ♂ 6 ♀, USNM, E of St Christopher, 644 m, 8 December 1969, *Oregon II* stn 10841. 34 ♂ 31 ♀, USNM, off St Christopher, 640-676 m, 20 May 1967, *Oregon* stn 6701. 2 ♀, USNM, E of Capesterre, Guadeloupe, 466-640 m, 16 July 1969, *Pillsbury* stn 936. 2 ♂ 7 ♀ syntypes, USNM 6907, S of Curaçao, 380 m, 18 February 1884, *Albatross* stn 2125. 2 ♂ 5 ♀ syntypes, USNM 6908, S of Curaçao, 380 m, 18 February 1884, *Albatross* stn 2125. 1 ♀, USNM, NW of Aruba, 622 m, 26 November 1970, *Oregon II* stn 11307.

WESTERN CARIBBEAN—2 ♂ 1 ♀, USNM, W of Rosalind Bank, 366 m, 7 June 1962, *Oregon* stn 3627. 2 ♂ 1 ♀, USNM, NE of Cayos Hobbies, 521 m, 25 October 1970, *Oregon II* stn 11220. 3 ♀, USNM, W of Rosalind Bank, 457 m, 24 August 1957, *Oregon* stn 1889. 32 ♂ 26 ♀, UMML, W of Quita Sueño Bank, 450-576 m, 31 January 1971, *Pillsbury* stn 1355. 5 ♂ 2 ♀, USNM, W of Quita Sueño Bank, 439-457 m, 21 May 1962, *Oregon* stn 3565. 1 ♀, USNM, SW of I de Providencia, 549 m, 13 September 1957, *Oregon* stn 1927. 1 ♂ 2 ♀, USNM, W of I de San Andrés, 549 m, 27 October 1970, *Oregon II* stn 11225. 1 ♀, USNM, W of Cayos de Albuquerque, 585 m, 27 October 1970, *Oregon II* stn 11226. 1 ♀, USNM, W of Cayos de Albuquerque, 192 m, 7 February 1967, *Oregon* stn 6444.

MEXICO—Quintana Roo: 1 ♂ 5 ♀, USNM, off I de Cozumel, 412-457 m, 16 March 1968, *Pillsbury* stn 602.

BELIZE—8 ♂ 2 ♀, YPM, off Glover Reef, 669 m, 29 April 1925, *Pawnee*. 4 ♂ 6 ♀, USNM, off Stann Creek, 457-732 m, 10 June 1962, *Oregon* stn 3635. 2 ♂ 3 ♀, USNM, off Jonathan Point, 348 m, 9 June 1962, *Oregon* stn 3643.

NICARAGUA—2 ♂ 2 ♀, USNM, NE of Islas del Maíz, 549-585 m, 23 May 1962, *Oregon* stn 3576.

PANAMA—8 ♂ 14 ♀, USNM, E of Península Valiente, 512 m, 25 May 1962, *Oregon* stn 3583. 6 ♂ 9 ♀, USNM, Golfo de los Mosquitos, 549 m, 31 May 1962, *Oregon* stn 3600. 1 ♂ 3 ♀, USNM, Golfo de los Mosquitos, 732 m, 31 May 1962, *Oregon* stn 3601. 2 ♀, USNM, NE of Belén, 439 m, 30 May 1962, *Oregon* stn 3592. 1 juv, USNM, off Punta Manzanillo, 421 m, 19 October 1965, *Oregon* stn 5740. 1 ♂, USNM, 5 July 1972, *Canopus*.

COLOMBIA—1 ♀, USNM, off Punta Broquelles, 732 m, 28 May 1964, *Oregon* stn 4902. 3 ♂ 3 ♀, USNM, N of Islas de San Bernardo, 549 m, 6 November 1970, *Oregon II* stn 11244. 7 ♂ 8 ♀, USNM, off Puerto Colombia, 366 m, 2 December 1968, *Oregon II* stn 10260. 4 ♀, USNM, W of Santa Marta, 631 m, 9 November 1970, *Oregon II* stn 11250. 1 ♂ 1 ♀, USNM, W of Ríohacha, 567-531 m, 30 July 1968, *Pillsbury* stn 781. 6 ♂ 3 ♀, UMML, W of Cabo de la Vela, 408-576 m, 29 July 1968, *Pillsbury* stn 776. 3 ♂ 7 ♀, USNM, W of Cabo de la Vela, 366 m,

2 June 1964, *Oregon* stn 4922. 21 ♂ 15 ♀, USNM, W of Cabo de la Vela, 439-448 m, 2 June 1964, *Oregon* stn 4923. 3 ♂ 2 ♀, USNM, off Cabo de la Vela, 485 m, 9 October 1965, *Oregon* stn 5689.

VENEZUELA—8 ♀, USNM, E of Península de Paraguaná, 421 m, 27 September 1963, *Oregon* stn 4406. 4 ♀, USNM, off Península de Paraguaná, 457 m, 4 October 1963, *Oregon* stn 4419. 4 ♀, USNM, NE of San Juan de los Cayos, 384-607 m, 26 July 1968, *Pillsbury* stn 753. 3 ♂ 9 ♀, USNM, off Península de Araya, 402 m, 20 October 1963, *Oregon* stn 4477. 2 ♂ 9 ♀, USNM, NE of Islas Los Testigos, 366-439 m, 24 September 1964, *Oregon* stn 5037. 10 ♂ 11 ♀, USNM, NE of Islas Los Testigos, 388-457 m, 23 September 1958, *Oregon* stn 2353. 5 ♂ 6 ♀, USNM, NE of Punta Araguapiche, 366 m, 3 November 1957, *Oregon* stn 1981. 3 ♂ 3 ♀, USNM, NE of Punta Araguapiche, 457 m, 3 November 1957, *Oregon* stn 1982.

GUYANA—1 ♂, USNM, off Waini Beach, 137 m, 4 November 1957, *Oregon* stn 1993.

Description.—Body robust, integument thick, and entirely covered by densely set, short setae (Figure 29). Rostrum almost reaching or slightly overreaching distal end of antennular peduncle, nearly horizontal and straight in large adults, somewhat shorter, elevated, and broadly convex dorsally almost to tip in young; tip saber or spear shaped, 0.2-0.3 rostrum length, longest in adult. Rostral plus epigastric teeth 10-12 (mode 11; $N = 200$); teeth regularly closer from epigastric to ultimate; epigastric tooth located almost at level of dorsal extremity of cervical sulcus and fourth rostral tooth near level of orbital margin. Adrostral carina slender, extending from orbital margin almost to apex of rostrum; postrostral carina strong, long, almost reaching posterior margin of carapace; small tubercle present behind postrostral carina; antennal carina short but prominent. Orbital spine short, broad basally; postorbital spine slender, rather short, located posterodorsal to base of antennal spine; latter longest of lateral spines on carapace; branchiostegal spine moderately long; hepatic spine relatively short; pterygostomian spine lacking. Cervical sulcus sinuous, deep, ending lateral to postrostral carina at about midlength of carapace; cervical carina sharp. Hepatic sulcus almost horizontal posteriorly, merging with depressed area ventral to hepatic spine, from there inclining anteroventrally, and ending in pit below branchiostegal spine; hepatic carina accompanying anterior portion of sulcus sharp and prominent; branchiocardiac carina indistinct or barely perceptible; submarginal carina well marked, subparallel to free ventral margin of carapace.

Eye (Figure 30*E*) with basal article produced distomesially into pubescent, broad scale, bearing spinelike distal projection; ocular peduncle short, cornea broad, greatest diameter slightly more than twice that of base of ocular peduncle, its proximal margin strongly slanting posterolaterally.

Antennular peduncle length equivalent to about 0.6 that of carapace; prosartema ending slightly proximal to distal margin of first article; stylocerite extending only to about 0.45 of distance between its proximal extremity and mesial base of distolateral spine, produced distally into short, rather blunt spine; distolateral spine slender and moderately long, sensibly overreaching distal margin of article. Antennular flagella (Figure 30*A*) rather broad proximally, subfiliform distally, markedly unequal in length, but both long, and increasing proportionately in length with age: dorsal flagellum about 1.4 times carapace length and ventral about 1.2 times carapace length, in shrimp 8.5 mm cl, and 3.5 and 2 times carapace length, respectively, in shrimp 32 mm cl (flagella incomplete in all larger animals examined). Dorsal flagellum with distal half of proximal portion bearing longitudinal row of combs of long setae on slightly concave ventral surface (Figure 30*D*) and stiff short setae on remaining surfaces; stiff setae increasingly sparse toward tip of flagellum. Ventral flagellum exhibiting strong sexual dimorphism: in mature male, proximal portion resembling bottle brush, with mesial surface flattened and bearing longitudinal band of stiff, dense setae with apices directed proximally (Figure 30*B*); lateral surface armed with numerous, simple setae directed distally (Figure 30*C*); dorsal and ventral surfaces bearing flexible, plumose setae, most thickly set in comblike clusters. In females, ventral flagellum with proximal portion covered by long flexible setae.

Scaphocerite exceeding antennular peduncle by as much as 0.2 of its own length; lateral rib ending in slender spine, falling short of distal margin of lamella. Antennal flagellum long, as much as 5 times total length of shrimp. Mandibular palp (Figure 31*A*) relatively short, extending to about distal extremity of ischiocerite, proximal article 1.25 times as long as wide; distal article only slightly longer and narrower than proximal one, tapering to blunt tip. Maxillae and first and second maxillipeds as figured (Figure 31*B-E*). Two rudimentary arthrobranchiae on somite VII, near base of coxa of first maxilliped (Figure 31*Dg-g*^{1}), both anterior and posterior arthrobranchiae on somite VIII, and podobranchia on

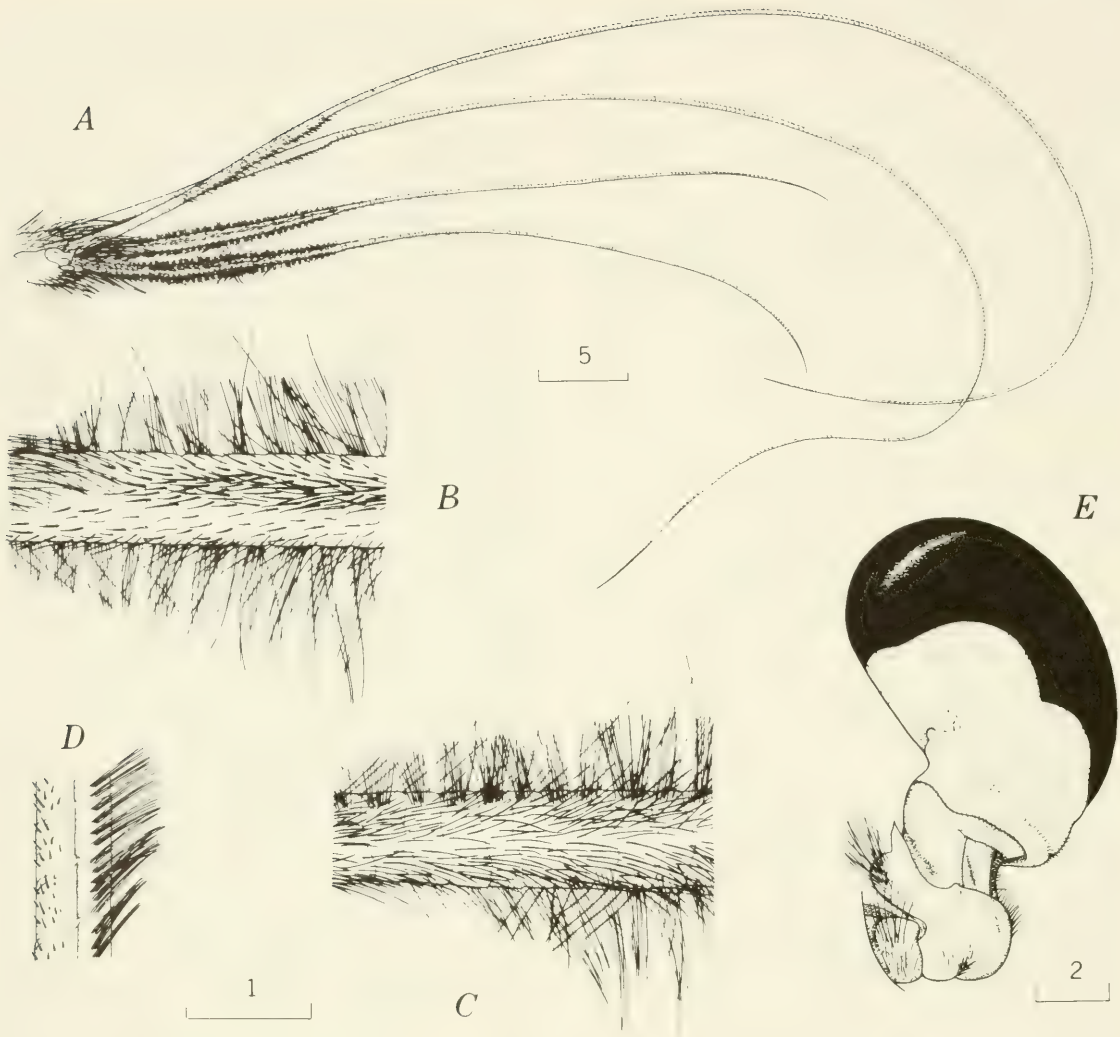

FIGURE 30.—*Pleoticus robustus*, ♂ 28 mm cl, south of Dry Tortugas, Fla. *A*, Antennular flagella. *B*, Mesial view of proximal part of ventral flagellum. *C*, Lateral view of same. *D*, Ventrolateral view of proximal portion (distal half) of dorsal flagellum. *E*, Eye, ♀ 34 mm cl, same locality.

corresponding second maxilliped; pleurobranchia, and anterior and posterior arthrobranchiae on somite IX (Figure 31*E*, *F*), pleurobranchiae present through somite XIV, and both arthrobranchiae through XIII. Third maxilliped exceeding antennular peduncle by at least 0.5 length of dactyl, or by dactyl and about 0.2 length of propodus.

First pereopod reaching between base and distal end of carpocerite. Second pereopod overreaching carpocerite by at least 0.5 length of dactyl, but by as much as entire propodus and 0.1 length of carpus. Third pereopod surpassing antennular peduncle by length of dactyl or by length of propodus and 0.2 that of carpus. Fourth pereopod extending to distal end of carpocerite or overreaching it by length of dactyl and 0.5 that of propodus. Fifth pereopod exceeding antennular peduncle by at least 0.5 length of dactyl or by length of dactyl and 0.4 that of propodus. Order of pereopods in terms of their maximal anterior extensions: first, second, fourth, third, and fifth. First pereopod with moderately long, sharp spine at distomesial extremity of basis and ischium, and midlength of merus. In female, coxa of third pereopod expanded into thick, roughly trapezoidal plate,

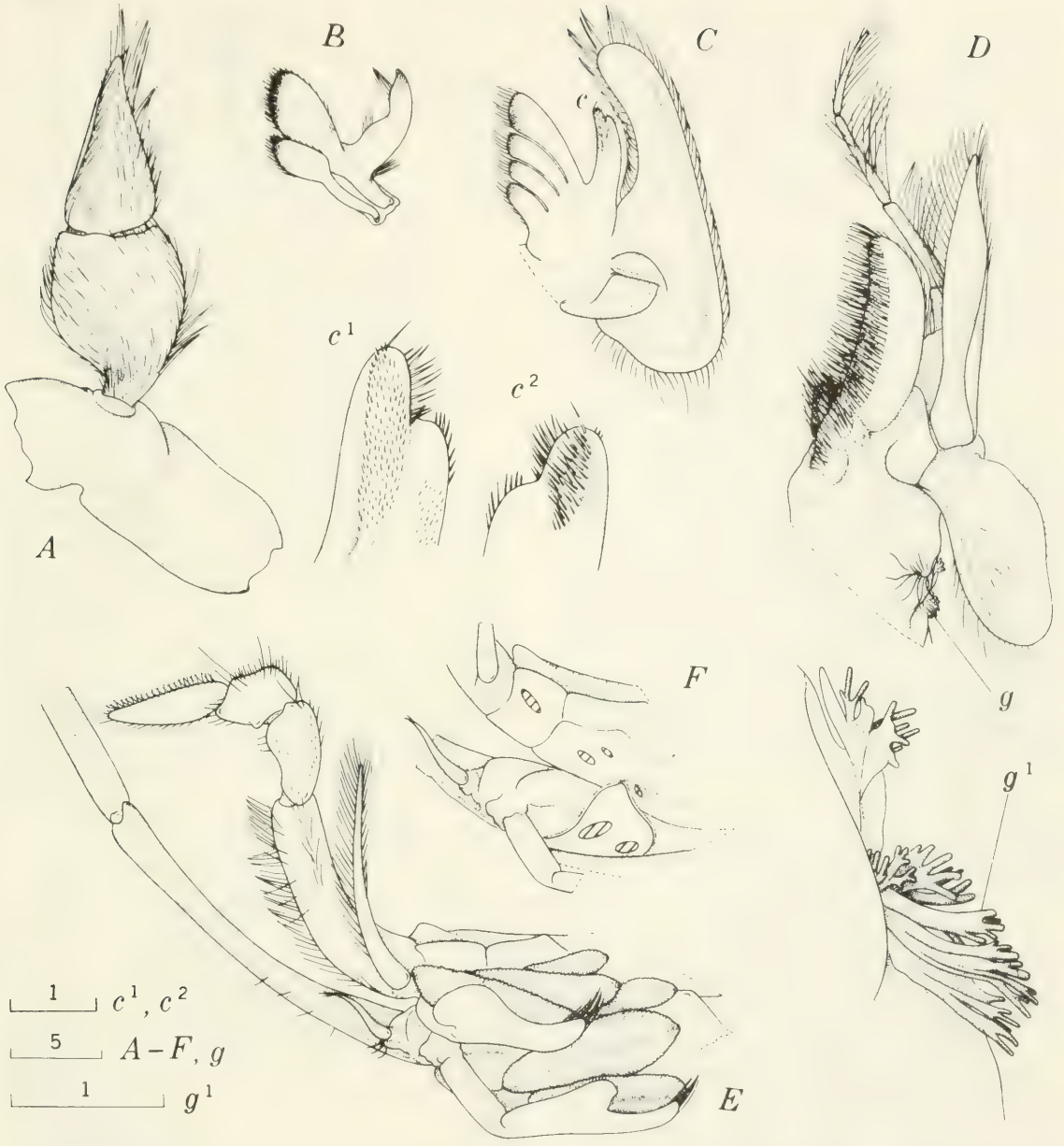

FIGURE 31.—*Pleoticus robustus*, ♀ 56 mm cl, off Dog Island, Lesser Antilles. *A*, Mandible. *B*, First maxilla. *C*, Second maxilla. *c*, Endite of basipodite. c^1, Enlargement of *c*, ventral view. c^2, Dorsal view. *D*, First maxilliped. *g*, Rudimentary arthrobranchiae. g^1, Enlargement of *g*. *E*, Second maxilliped and proximal portion of third. *F*, Somites VIII and IX with proximal portions of second and third maxillipeds, showing attachments of gills.

raised in strong, densely setose prominence on ventral surface. Coxa of fifth pereopod in male bearing blunt spine on anteromesial margin; in female, coxa produced into setose, short plate.

Abdomen with middorsal carina from third through sixth somites, carina rounded on third, sharp and high from fourth posteriorly; sixth somite with small spine at posterior end of carina and paired, posteroventral spines. Telson with median sulcus rather shallow, short, occupying

about 0.35 length of telson, flanked by low carinae, latter becoming sharp posteriorly, reaching base of lateral spines; length of spine 1.1 to 1.5 times width of terminal portion at base; terminal portion length 3 to 4 times basal width. Mesial ramus of uropod overreaching apex of telson by about 0.2 of its length; lateral ramus, in turn, overreaching mesial by as much as 0.25 of its own length, and bearing minute, terminal, distolateral spine.

Petasma (Figure 32*A, B*) cincinnulate along entire median line, with distal margin spinulous; midrib of dorsolateral lobule broadest proximally, and ending distally in narrow, sometimes sinuous tip; ventrolateral lobule almost entirely sclerotized, but produced distally into rather flexible, elongate flap, strongly inclined toward median lobe; ventral costa with free terminal part curved dorsally and armed with minute spines on distal margin.

Appendix masculina (Figure 32*C, D*) elongate, deeply excavate ventromesially for reception of appendix interna, broad proximal part raised in longitudinal, lateral rib extending to base of narrower distal part; strong dorsal thickness along distal part curving around terminal margin, there bearing tuft of rigid setae. Appendix interna considerably shorter than appendix masculina and consisting of short bulbous basal portion and elongate, narrow but thick distal portion. Ventrolateral spur abruptly narrowing slightly distal to midlength, becoming fingerlike.

Thelycum (Figure 33*A*) microscopically setose-punctate (Figure 33*B*), with paired subtriangular projections on anteriormost part of sternite XIV, usually inclined anteriorly, overlapping posterior margin of sternite XIII; posterior part of sternite XIV strongly bulging, often bearing midlongitudinal groove. Median plate of sternite XIII delimited anteriorly by paired deep depressions, and armed with strong anteromedian rib; sternite XII with central elevation, and paired, transverse marginal ridges overlapping sternite XIII.

Color.–Both coloration, as previously indicated by various authors, and color pattern are very variable. Burkenroad (1936) described fresh, though dead, juveniles, caught in the waters off Alabama, as follows: "Eyes deep reddish-brown with greenish reflections; gastric gland grayish-brown with light yellow-green flecks, stomach red; body pale orange-red, with a band of deeper salmon on the posterior part of each pleonic tergum; an iridescent blue-green area on the dorsum of each pleonic segment and of the telson." Springer (1951b) indicated that shrimp taken in the northern Gulf of Mexico were "brick red as they come from the water." Anderson and Bullis

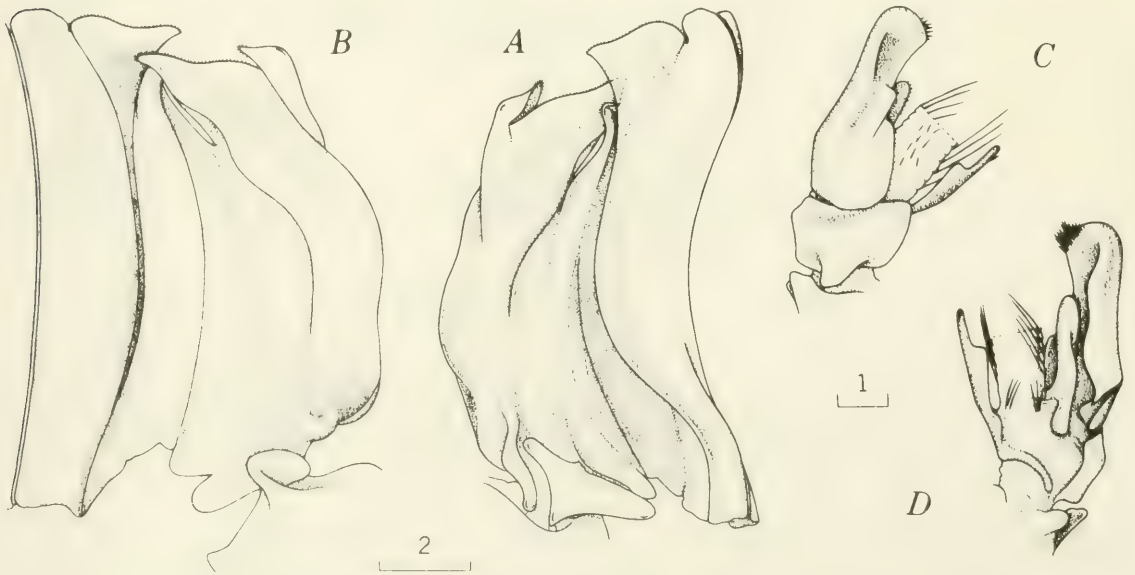

FIGURE 32.—*Pleoticus robustus*, ♂ 32 mm cl, east of Península Valiente, Panama. *A*, Petasma, dorsolateral view of left half. *B*, Ventrolateral view (extended). *C*, Right appendices masculina and interna, lateral view. *D*, Mesial view.

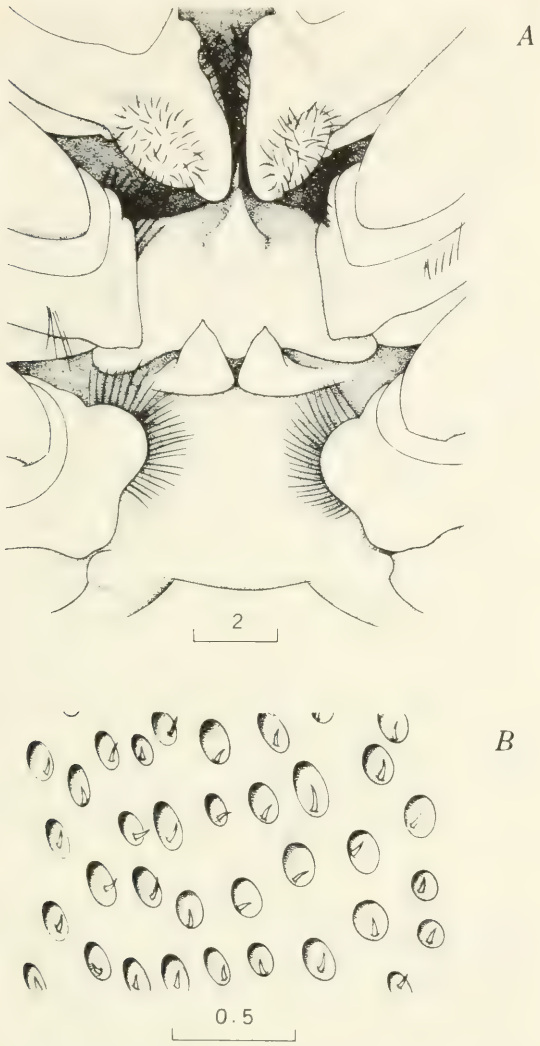

FIGURE 33.—*Pleoticus robustus*, syntype ♀ 49 mm cl, south of Curaçao. *A*, Thelycum, ventral view. *B*, ♀ 61 mm cl, west of Ríohacha, Colombia. Portion of sternite XIV showing seta-bearing depressions.

(1970) found that in animals observed from a submarine the "Color varied from grayish pink to red—similar to color observed on trawl-caught specimens." A diel color change was pointed out by Bullis (1956), who stated "nighttime catches are typically bright red, while catches landed during daylight hours are a light pink." Recently, García del Barco (1972) has confirmed this circadian variation.

My examination of large quantities of freshly collected animals during a 1969 cruise of the *Oregon II* in the Caribbean (Puerto Rico to Antigua) corroborated earlier observations of the great variation in this character, and disclosed the existence of many color patterns. The overall body color ranges from off white through pink and salmon to deep red, and the color pattern may consist of a few bright lines—mostly on various carinae—or even an abundance of strong markings. Opaque white and, particularly, reddish with white markings individuals were very common, whereas salmon ones, apparently similar in color to those shrimps from the northern Gulf of Mexico described by Burkenroad, were infrequent.

Descriptions of three color phases observed follow:

Pink-red phase: Body pink, marked with red and white. Gastric region intense pink; rostrum brilliant red with tip paler; anterior rostral teeth with bases red and apices light, but teeth posterior to orbital margin with brilliant deep red apices; small white patch in area between orbital, postorbital, and antennal spines; cardiac region light red; anteroventral border as well as antennal and cervical carinae and contiguous spines deep red; longitudinal opaque white stripe tapering from anteroventral margin (dorsal to branchiostegal spine) to depressed area below hepatic spine, from there broadening abruptly along entire cervical sulcus, then tapering again to about level of third pereopod, there forming narrow, short stripe, continuing along posterior margin of carapace then recurving anteriorly, parallel to ventral margin, to level of base of second maxilliped, ending there in elongate white patch; deep red stripe inserted between arms of pink one. Abdomen light pink anteriorly, increasingly deep pink posteriorly, turning red on sixth somite; first five somites with posterior margin of tergum bordered by transverse red band, and posterior margin of pleuron with white band continuing anteriorly onto ventral margin; middorsal carina as well as posterior and ventrolateral margins of sixth somite brilliant red. Telson light red, with carinae, lateral margins, and transverse band proximal to terminal portion deep red. Basal podomere of uropod pink with lateral margin red; lateral ramus intense pink except for deep red tip; mesial ramus with pink proximal portion followed by white transverse band and latter, in turn, by red marking covering distal portion except for white mesial patch. Antennular peduncle light red, but apex of stylocerite and distolateral

spine brilliant red, and prosartema pink; flagella red proximally fading to pink distally. Antenna pink. Third maxilliped and pereopods with coxa and basis white, remaining podomeres reddish. Pleopods with basis white but bearing pink semicircular, lateral patch; exopods white proximally, with red and pink transverse bands on midportion, and white distal patch; endopods white with pink band at midlength. Eye with peduncle white, and separated from cornea by two lines, proximal pink and distal red; basal article pink.

Salmon phase: Carapace anterior to cervical sulcus deep salmon, cardiac region, and ground color of abdomen pale salmon; rostrum (except for white tip) and branchiostegite bright reddish orange, that on branchiostegite sharply delimited dorsally along hepatic sulcus and branchiocardiac carina; apices of rostral teeth and spines, as well as postrostral and cervical carinae deep orange-red; bases of teeth and spines, and cervical sulcus opaque white. Tergum of first through fifth abdominal somites with posterior, transverse band of reddish orange, band broad on middorsal portion, tapering ventrally to base of pleuron, from there extending along posterior margin and onto ventral margin; middorsal carina as well as posterior and ventrolateral margins of sixth somite deep reddish orange. Telson with ground color deep salmon, except for yellowish white basal portion; lateral portion of margins and paired carinae bright orange-red, giving rise on each side to angle with vertex on spine. Pereopods with coxa and basis white, and remaining podomeres salmon with longitudinal orange-red strip. Pleopods yellowish, but basis with roughly semicircular lateral white patch subtended by bright reddish orange stripe on lateral margin. Uropod mostly salmon; lateral ramus with distalmost portion bright red and mesial ramus with tip white.

Opaque white phase: Ground color opaque white with very pale salmon suffusion, more intense on rostrum; however, tip of rostrum, teeth and adrostral carina corneous; cardiac region grayish white, and entire branchiostegite milky white; branchiostegal and hepatic spines as well as cervical and postrostral carinae orange-red; longitudinal streak of orange-red extending posteriorly from dorsal end of cervical carina well beyond midlength of carapace. Pleura of first five abdominal somites with milky white U-shaped band following contour of margin; middorsal carina and posterior and ventrolateral margins of sixth somite orange-red. Telson almost white with median sulcus orange-red. Lateral ramus of uropod with oblique, milky white stripe at base of distal fourth, and subtended distally by intense salmon colored band and this, in turn, by white tip; mesial ramus with large, proximomesial, suboval, milky white patch bounded laterally by salmon band, and with distalmost portion milky white. Antennular peduncle deep salmon proximally, becoming pink distally; prosartema, antennular flagella, and antenna pink. Third maxilliped and pereopods with coxa and basis white, and remaining podomeres white with very light pink suffusion. Pleopods pinkish white bearing milky white, semicircular, lateral patch. Ocular peduncle white, and bearing orange-red stripe along border with cornea.

Maximum size.–The largest male examined by me has a carapace length of 42 mm, about 173 mm tl, and the largest female, 61.5 mm cl, about 219 mm tl; however, Klima (1969), in his work on length-weight relation, recorded larger specimens of both sexes, a male within the range of 180-184 mm tl and a female within 225-229 mm tl.

The sizes at which maturation occurs were determined by Anderson and Lindner (1971) to be at about 125 mm tl in males and about 155 mm tl in females.

Geographic and bathymetric ranges.–Pleoticus robustus ranges (Figure 34) from immediately south of Martha's Vineyard, Mass. (40°00′15″N, 70°54′00″W), through the Gulf of Mexico, and the Caribbean to French Guiana (07°05′N, 52°47′W), occurring on the upper continental slope at depths between about 180 and 730 m (Figure 9). It has been found only occasionally north of Cape Hatteras, and seems to be scarce off the Guianas. Inasmuch as this species has not been reported from Brazilian waters, French Guiana is cited here as the southernmost limit of the species on the basis of samples taken during the *Oregon* cruises off northeastern South America. The southern range of the species given by Bullis and Cummins (1963) was based on the same collections; consequently their statement that the royal red reaches Brazil should be understood to mean that it extends to about the border between French Guiana and Brazil.

The highest concentrations of *P. robustus*—off the northeast coast of Florida and in the north-

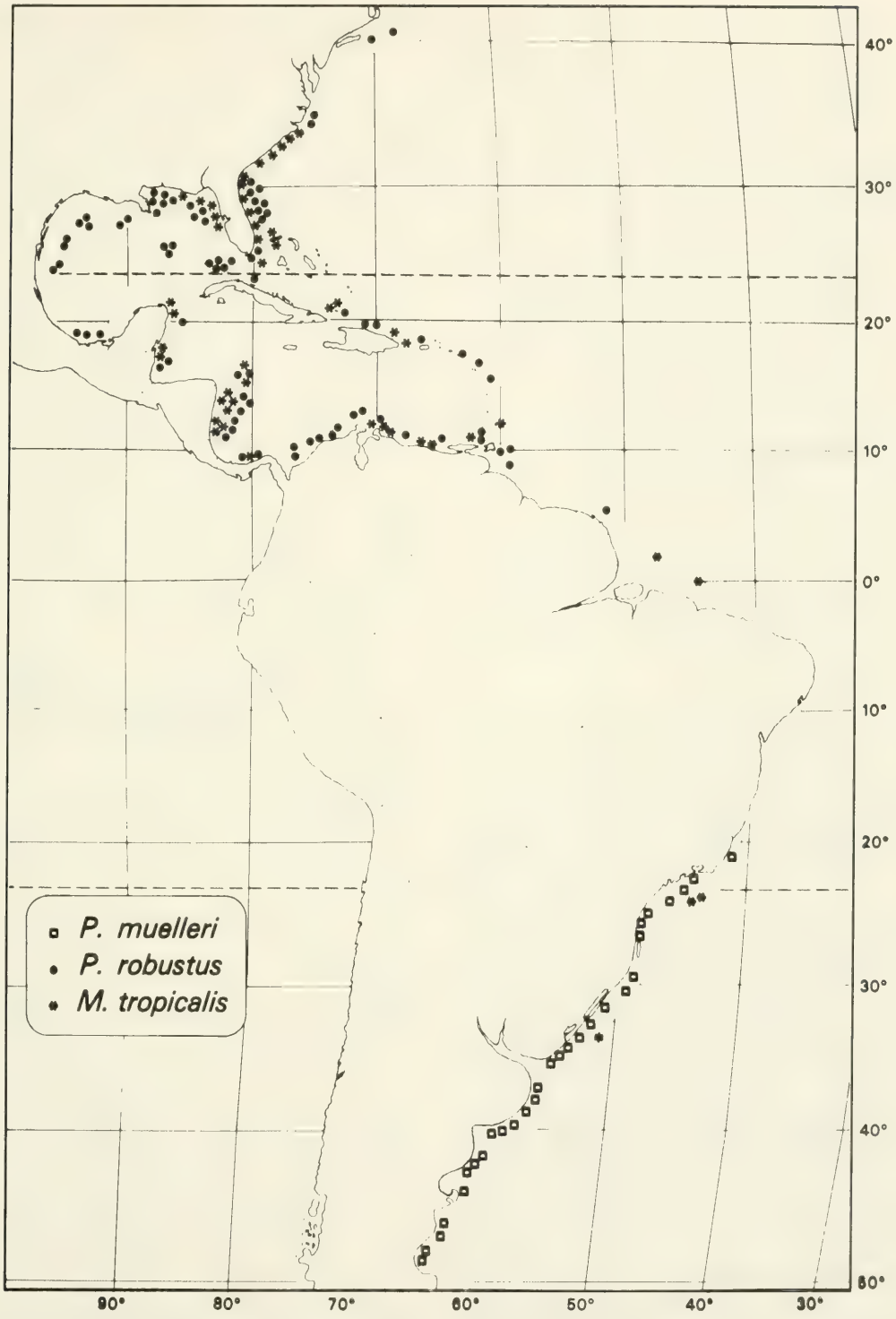

FIGURE 34.—Ranges of *Pleoticus muelleri*, *Pleoticus robustus*, and *Mesopenaeus tropicalis* based on published records and specimens personally examined.

eastern part of the Gulf of Mexico—occur at depths between 250 and 475 m. The species is scarce in less than 256 m, and not abundant at depths greater than 500 m. If the data are correct, the male found in 137 m off Guyana at *Oregon* stn 1993 represents an extremely rare occurrence of the shrimp in waters shallower than 180 m, as does the presence of the species at 70 m (at *Oregon* stn 2669, 18°31′N, 66°47.5′W, north of Puerto Rico), reported by Bullis and Thompson (1965). Although Roberts and Pequegnat (1970) stated that this shrimp has been found at depths as great as 500 fm (915 m), there is no precise record of its presence below 400 fm (732 m). Their statement seems to have been based on a catch from the *Alaminos,* in 289-472 fm (529-863 m); however, their remaining records, as well as those of all others, suggest that the specimens obtained in that haul were caught in the shallower part of the depth range cited.

Throughout the Caribbean and northeastern South America, the royal red shrimp seems to be rather sparsely distributed; various explorations by the *Oregon* and *Oregon II* in the region have indicated a dense concentration only off Cabo de la Vela, Colombia.

Affinities.–Pleoticus robustus can be separated from *P. muelleri,* the only other western Atlantic representative of the genus, by the following characteristics: the densely pubescent body, the relatively short prosartema, which does not overreach the distal margin of the first antennular article, the presence of a branchiostegal spine, the lack of an orbital spine, and the disposition of the submarginal carina which is subparallel to the free border of the carapace along its entire length. The external genitalia of the two species are also quite different: whereas in the petasma of *P. robustus* the row of cincinnuli occupies the entire median line, the ventromedian lobule is flexible and entire distally, and the ventral costa is plain, in *P. muelleri* the row of cincinnuli extends only along the proximal 0.4 of the median line, the ventromedian lobule is produced distally in cornified oval and hooklike projections, and the distal part of the ventral costa bears a flange along the inner border. Also, the thelycum of *P. robustus* exhibits a pair of anterior triangular projections on the flexible anterior part of sternite XIV, and a median ridge on sternite XIII, whereas that of *P. muelleri* bears nothing more than a pair of minute tubercles on the heavily sclerotized anterior part of sternite XIV, and a strong median projection on sternite XIII.

Spermatophore.–Compound spermatophore (as attached to female) consisting of broad, dorsoventrally depressed geminate body, with conspicuous transverse fold at about midlength, and bearing anterolateral wings; also provided with sculptured lateral flaps, and produced posterolaterally in short flanges (Figure 35).

Ventral and lateral walls of each spermatophore (Figure 36*A*) thick, opaque, fusing imperceptibly, their anterior margins broad and perpendicular to medial line. Spermatophore lacking anterior lobe, deeply concave at base of wing, there bearing conspicuous constriction; transverse angular fold present at about midlength, followed by depressed caudal half. Dorsomesial wall (Figure 36*C*) largely translucent, with globular anterior evagination (Figure 36*B*) markedly expanding lumen of sperm sac; posterior part of latter attenuated caudally by close proximity of opposing walls. Flap broad anteriorly and merg-

FIGURE 35.—*Pleoticus robustus,* compound spermatophore attached to female, ♀ 44 mm cl, west of Quita Sueño Bank, western Caribbean (setae omitted).

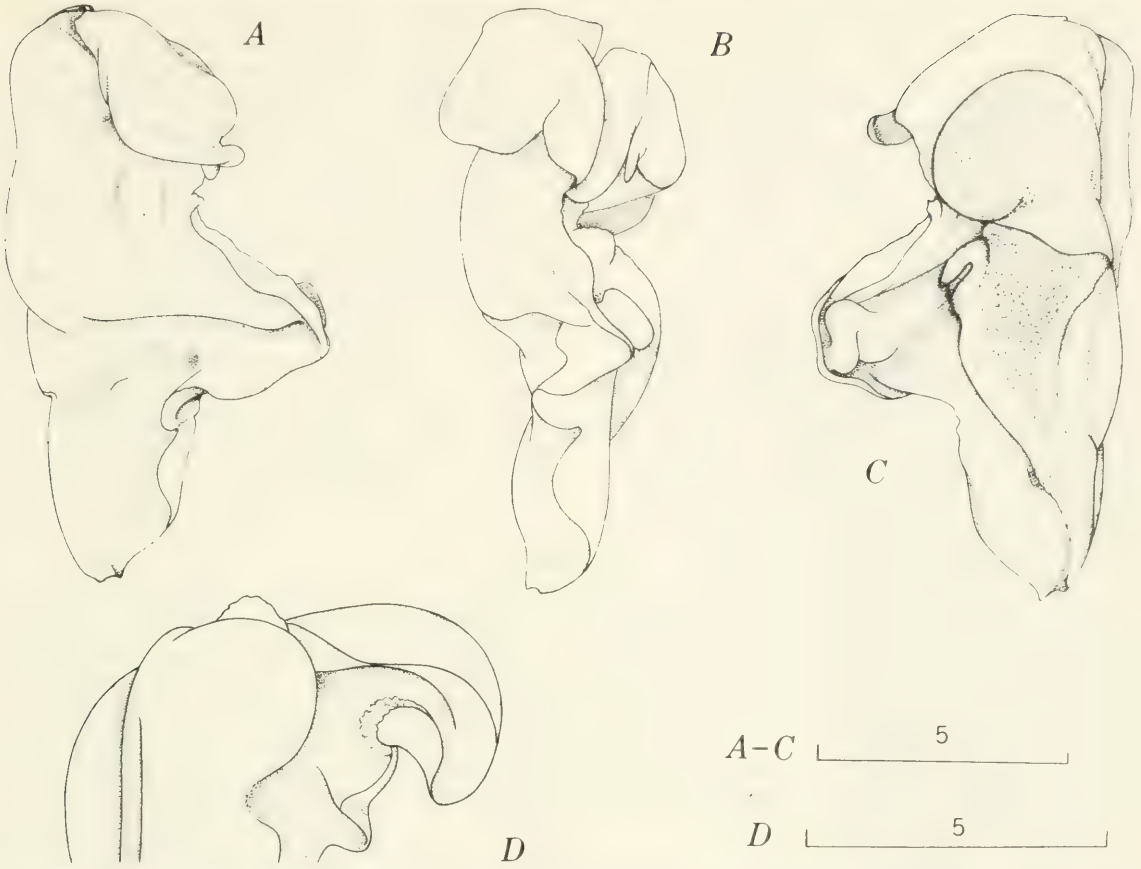

FIGURE 36.—*Pleoticus robustus*, ♂ 37 mm cl, east of St Lucie Inlet, Fla. *A*, Left spermatophore dissected from terminal ampulla, ventrolateral view. *B*, Lateral view. *C*, Dorsal view. *D*, ♂ 38 mm cl, off St Augustine, Fla. Distal portion of left spermatophore (wing extended).

ing insensibly with lateral base of flange. Wing (Figure 36*D*) heavy, opaque, with broad base forming rounded lobe continuous with lateral wall, and tapering to short, blunt tip. Flange short, broadly subelliptical. Dorsal plate nearly triangular, anteriorly fitting snugly into deep groove of dorsomesial wall.

Compound spermatophore applied to female with anterior margin lying approximately at posterior margin of gonophores, and sperm masses—protruding through dorsomesial walls (apparently torn by forced release of those masses during mating)—lodged in paired concavities of sternite XIII. Bases of the wings attached to sternite XIII, their distal parts resting on same sternite, and on ventral articular membranes of fourth pereopods. Lateral flaps affixed to sternite XIV, and just posterior to transverse folds of sacs, geminate body sloping caudodorsally over bulge of sternite XIV; adjoining flanges resting on posterior thoracic ridge. Wings and lateral flaps lie under (dorsal) setose coxae of fourth and fifth pereopods, respectively, which also aid in securing compound spermatophore on female. Dorsal plates, subjacent (dorsally) to caudal part of sacs, directly anchored to sternite XIV, thus helping to hold spermatophore in place.

The exceedingly large spermatophores of this shrimp appear to become attached to the female more firmly than those of many other penaeids with open type thelyca. This statement is based on the observation that females with attached spermatophores are frequently found in collections, whereas in other species with open type thelycum such females are rarely encountered. Most of the compound spermatophores that I have

detached from impregnated females are practically empty. This suggests that the sperm are released with the entire spermatophore present, i.e., that the spermatophore is not torn or split leaving the sperm masses with the paired wings flanking them on the female while the geminate body and adjoining flanges fall away, as seems to occur in some members of the subgenus *Litopenaeus*, genus *Penaeus*.

Reproduction.–Anderson and Lindner (1971) reported that on the St. Augustine Grounds, *P. robustus* probably spawns throughout the year, with a peak between January and May. Recruitment begins when the shrimp are approaching 1 yr of age and are less than 100 mm tl; maturity is reached in about 3 yr. Most shrimp on the grounds are mature, and the life span appears to be no less than 5 yr.

The larvae of *P. robustus* are unknown. Burkenroad (1936) identified as "juveniles" the only postlarvae of the species ever recorded, specimens that I have examined. Curiously, Anderson and Lindner (1971) found neither larval nor postlarval stages in a large number of plankton samples collected over an extensive area seaward of the St. Augustine Grounds. They stated that only a single larva was considered as possibly belonging to *"Hymenopenaeus."*

Ecological notes.–In the northestern Gulf of Mexico and off the southeastern coast of the United States, this shrimp has been found within a temperature range of 5°-15°C, and is commercially abundant betwen 9° and 12°C (Bullis 1956; Bullis and Cummins 1963). The preference of *P. robustus* for this range of temperature was revealed by the observations of Bullis and Cummins, who stated that within 1 or 2 days after two incursions of cold bottom water off the northeast coast of Florida, shrimp moved inshore to waters 75 m shallower than those where they had been observed previously. Later, Roe (1969) reported that the maximum densities of this shrimp is in water temperatures of 9° to 10°C.

Commercial concentrations of royal red have been reported (Bullis 1956; Bullis and Rathjen 1959; Roe 1969) to occur on the following types of bottoms: blue-black terrigenous silt and silty sand off the Mississippi River Delta; whitish, gritty, calcareous mud off Tortugas; and basically similar sand or silty sand (called "green mud" by the fishermen) off the northeast coast of Florida.

Anderson and Bullis (1970) presented direct observations of this shrimp made from the submarine *Aluminaut* off Daytona Beach, Fla., at a depth of 459 m. They stated that "The bottom was remarkably free from obstructions and consisted of a grayish, loosely constituted sediment that readily clouded the water at the least disturbance. It was formed into a myriad of shallow depressions and mounds, pitted with holes. . . . Bottom photographs had previously indicated that royal-red shrimp stayed on the sea-floor surface, but we saw numerous shallow furrows (1 to 3 feet long) in the bottom in which royal-red shrimp were partly buried. They apparently do not burrow as deeply or completely as do brown and pink shrimp. We believe the shrimp plow into the bottom in search of food rather than protection, and that this feeding activity produces the grooves or furrows."

Remarks.–Smith (1885) cited 14 males and 4 females in USNM lots 6907 and 6908. My examination of this material has shown that the first lot consists of 2 males and 7 females, but the second lot includes 2 males and 5 females of *"Hymenopenaeus" robustus* and 1 female of *Penaeopsis serrata* (Bate 1881). Consequently Smith's statement is in error since there are only 4 males and, furthermore, the total number of females (including that of the latter species) must have been either 13 or 12 if one of them is missing from the lots. In the original description of the species, Smith stated that the proximal portion of the ventral antennular flagellum "is densely hairy in the male"; however, the marked difference that occurs between the pubescence of the flagellum in the male and the female has not been cited in subsequent morphological studies of the shrimp. Here, for the first time, detailed accounts of the setation of the ventral flagellum in both sexes are presented.

The petasma of *P. robustus* has been described previously by various investigators. Smith (1885) gave the first brief account. Later, A. Milne Edwards and Bouvier (1909) described and illustrated it in more detail; however, the two figures presented by them include several inaccuracies which were pointed out by Burkenroad (1936). In the same publication, the latter gave an accurate description of this structure. More recently, Roberts and Pequegnat (1970) presented observations as well as a sketch of the petasma, and Anderson and Lindner (1971) have provided the

most complete illustration available. The account of the petasma herein, utilizing Kubo's (1949) terminology, is given in order that comparisons of this species with others treated in this work may readily be made.

Economic importance.–*Pleoticus robustus* is the only deep-water penaeoid in the western Atlantic that is now commercially exploited.

This large wide ranging shrimp has been found in commercial quantities only in three areas off the coast of the United States:

1. off northeast Florida on the St. Augustine Grounds
2. south to southwest of Dry Tortugas Islands
3. southeast of the Mississippi River Delta to off Tampa Bay.

The commercial potential of the species was reported by Springer (1951b) and Springer and Bullis (1952) on the basis of its abundance off the Mississippi Delta. Subsequent explorations in the northern and northeastern Gulf of Mexico confirmed previous findings, and disclosed the concentration off the Dry Tortugas (Springer and Bullis 1954; Bullis 1956). Later, Bullis and Rathjen (1959) investigated the density of the populations off the southeast Atlantic coast of the United States and indicated the high potential of the St. Augustine Grounds, the exploitation of which began in 1962 (Cummins and Rivers 1962). The grounds in the northeastern Gulf of Mexico remained unexploited until this decade, when fishing was initiated. Total landings of royal red shrimp in 1976 (Anonymous 1977) amounted to 167,000 pounds (75,751 kg), heads-off, caught almost entirely off northwest Florida.

Pleoticus muelleri (Bate 1888)

Figures 9, 34, 37-42

Philonicus mülleri Bate 1888:275, pl. 39, fig. 1-2 [syntypes: 5 ♂ 25 ♀, BMNH, off Montevideo, Uruguay, 35°02′S, 55°15′W, 13 fm (24 m), 25 February 1876, *Challenger* stn 321]. Fowler 1912:543.

Pleoticus mülleri. Bate 1888:939. Berg 1898:38. Fesquet 1933:6, fig. 1-4, pl. 1-8; 1936:61. Barattini and Ureta 1960:49.

Parartemesia carinata Bouvier 1905b:748 [syntypes: 1 ♂ 3 ♀, MP 59, off mouth Río de la Plata, 35°42′S, 56°20′W, 44 fm (80 m), *Hassler*. 1 ♀, Río de la Plata, Montevideo, 7 fm (13 m), *Hassler*].

Haliporus carinatus. Bouvier 1906b:4.

Haliporus mülleri. Bouvier 1908:80. A. Milne Edwards and Bouvier 1909:214, fig. 38-44, pl. 2, fig. 9-10. Pesta 1915:102.

Hymenopenaeus mülleri. Burkenroad 1936:103. Fesquet 1941:64. Rioja 1941:200, fig. 13, 17; 1942:659, fig. 20, 21, 30, 31. Anderson and Lindner 1945:288. López 1954:46. Popovici and Angelescu 1954:505. Lindner 1957:4. Angelescu and Boschi 1960:1, fig. 4, 10-16, pl. 1, 2, 5, 6. Eldred and Hutton 1960:91. Boschi and Angelescu 1962:1, fig. 1-17, pl. 1, 2. Boschi 1963:5, fig. 4. Mistakidis and Neiva 1964:471. da Silva 1965:4. Tremel and Mistakidis 1965:2. Mistakidis 1965:1. Neiva and Mistakidis 1966:4, fig. 4a, b. Mistakidis and Neiva 1966:434. Idyll 1969:642. Pérez Farfante 1970:13, fig. 3I-K. Iwai 1973:44.

Hymenopendeus mülleri. Carcelles 1947:4, pl. 1, fig. 2.

Hymenopenaeus muelleri. Boschi 1964:38. Holthuis and Rosa 1965:1. Boschi 1966:452. Boschi and Mistakidis 1966:1. Boschi and Scelzo 1969a:3; 1969b:152, pl. 1. Boschi 1970:65; 1974:3. Scelzo and Boschi 1975:193. Boschi and Scelzo 1976:1. Boschi 1976:63.

Camarão barbado. Tremel et al. 1964:8.

Vernacular names: langostino, langostín (Uruguay, Argentina), camarão de Santana, lagostinho da Argentina, camarão vermelho, camarão barbado, camarão ferro (Brazil).

Material

BRAZIL—Espírito Santo: 2 ♀, USNM, off Praia de Santana, June 1962, G. de Souza Neiva. Rio de Janeiro: 2 ♀, USNM, off Macaé, 23 m. Superintendência do Desenvolvimento da Pesca, Seçao de Pesquisas. 9 ♀, USNM, Ilha dos Franceses, Cabo Frio, 50 m, 17 October 1975, Staff Instituto de Pesquisas da Marinha, Estaçao de Biologia Marinha. 4 ♀, YPM, off Rio de Janeiro, May 1934, M. W. Feingold. 1 ♀, USNM, off Ilha Grande, 23 m, 8 December 1961, *Calypso* stn 115. 3 ♀, USNM, off Baía da Ilha Grande, 36 m, 9 December 1961, *Calypso* stn 122. São Paulo: 3 ♂, USNM, Ubatuba, 15 m, 10 April 1972, J. de Abreu. 1 ♂ 5 ♀, MP, S of Ilha de São Sebastiaõ, 25 m, 11 December 1961, *Calypso* stn 135. 15 ♂ 9 ♀, USNM, Baía de Santos, 6 September 1964, G. Vazzoler. 4 ♂ 3 ♀, USNM, Baía de Santos, 29 September 1964, G. Vazzoler. 3 ♂ 3 ♀, USNM, Baía de Santos, 1 October 1962, G. de Souza Neiva. 3 ♂ 5 ♀, USNM, Farol de Moela, Santos, 9 September 1964, G. Vazzoler. Paraná: 1 ♀, USNM, off Paranaguá, Ex. H. Jakobi. Santa Catarina: 37 ♂ 47 ♀, MP, off Ensenada de Tijucas, 18 m, 16 December 1961, *Calypso* stn 149. 5 ♀, USNM, Armação de Piedade, 19 November 1965,

E. Tremel. Rio Grande do Sul: 16 ♂ 14 ♀, MP-USNM, off Barra Casino, 21 m, 18 December 1961, *Calypso* stn 153. 1 ♂ 1 ♀, USNM, Xuí, 19 m, 8 January 1962, *Calypso* stn 183.

URUGUAY—8 ♂ 9 ♀, MP-USNM, off Punta del Palmar, Rocha, 20-22 m, 21 December 1961, *Calypso* stn 156. 26 ♂ 35 ♀, MP, off Punta del Este, 57 m, 21 December 1961, *Calypso* stn 157. 1 ♂, MP, N of La Paloma, 33 m, 21 December 1961, *Calypso* stn 158. 34 ♂ 63 ♀, MP-USNM, N of Cabo Santa María, 25 m, 8 January 1962, *Calypso* stn 182. 26 ♂ 48 ♀, MP-USNM, off Laguna Rocha, 30 m, 22 December 1961, *Calypso* stn 161. 7 ♂ 7 ♀, MP, off Punta Negra, 18 m, 27 December 1961, *Calypso* stn 167. 1 ♂ 3 ♀, MP, off Maldonado, 115 m, 21 December 1961, *Calypso* stn 160. 1 ♂ 5 ♀, ANSP, Bahía Maldonado, W. H. Rush. 8 ♂ 15 ♀ syntypes of *Philonicus mülleri*, BMNH, off Montevideo, 13 fm (24 m), 25 February 1876, *Challenger* stn 321.

ARGENTINA—1 ♂ 3 ♀ syntypes of *Pararternesia carinata* Bouvier, MP 49, mouth of Río de la Plata, 44 fm (80 m), *Hassler*. 13 ♂ 11 ♀, YPM, "Buenos Aires," 15 June 1936. 2 ♀, USNM, Mar del Plata, 15 December 1922, H. M. Smith. 2 ♂ 2 ♀, UMML, Mar del Plata, January 1959 Ex. E. Boschi. 2 ♀, Quequén, 7 January 1924, G. Haedo. 1 ♀, USNM, Puerto Madryn, Chubut, Ex. Museo Argentino de Ciencias Naturales. 1 ♂ 2 ♀, Rawson, Chubut, November 1963, E. Boschi.

Description.–Body robust, integument thick, polished except for dorsally pubescent rostrum, narrow bands of setae flanking middorsal carina of sixth abdominal somite, and similar bands along borders of median and lateral sulci of telson; also broad bands of longer setae flanking paired longitudinal ridges of mesial ramus of uropod. Rostrum horizontal (Figure 37), straight, rather short, not reaching beyond distal 0.3 length of second antennular article, with dorsal margin slightly convex, and ventral margin almost straight, occasionally with apical concavity. Rostral plus epigastric teeth 7-13 (mode 9; $N = 200$), epigastric tooth separated from first rostral by interval similar to that between first and second, epigastric tooth located at level of dorsal extremity of cervical sulcus and usually fourth tooth at level of orbital margin. Adrostral carina slender, extending from orbital margin to base of ultimate tooth; postrostral carina strong, long, almost reaching posterior margin of carapace, where flanked by paired depressions. Orbital spine short; broad postorbital, antennal, and hepatic spines moderately long and sharp; pterygostomian and branchiostegal spines lacking. Cervical sulcus only slightly sinuous, deep, with dorsal extremity situated relatively far from postrostral carina; cervical carina sharp. Hepatic sulcus nearly horizontal from posterior end to depression below hepatic spine, there turning anteroventrally and reaching to pterygostomian region; hepatic carina accompanying anterior part of sulcus sharp; branchiocardiac carina lacking; submarginal carina well marked, horizontal posteriorly, turning anteroventrally at about midlength of carapace and then continuing close to free ventral margin of carapace almost to pterygostomian region.

Eye (Figure 38) with basal article produced distomesially into pubescent, broad scale; ocular peduncle short; cornea broad, greatest diameter slightly less than 2 times that of base of ocular peduncle, its proximal margin moderately slanting posterolaterally.

Antennular peduncle length equivalent to about 0.6 that of carapace; prosartema long, reaching distal 0.4 of second antennular article; stylocerite spiculiform distally, moderately long, its length about 0.65 of distance between its proximal extremity and mesial base of distolateral spine; latter sharp and long. Dorsal flagellum filiform, ventral flagellum broad proximally, tapering distally, and bearing marginal (lateral and mesial) patches of long setae proximally, latter continuous with single row distally; in shrimp 24 mm cl, ratio of length of

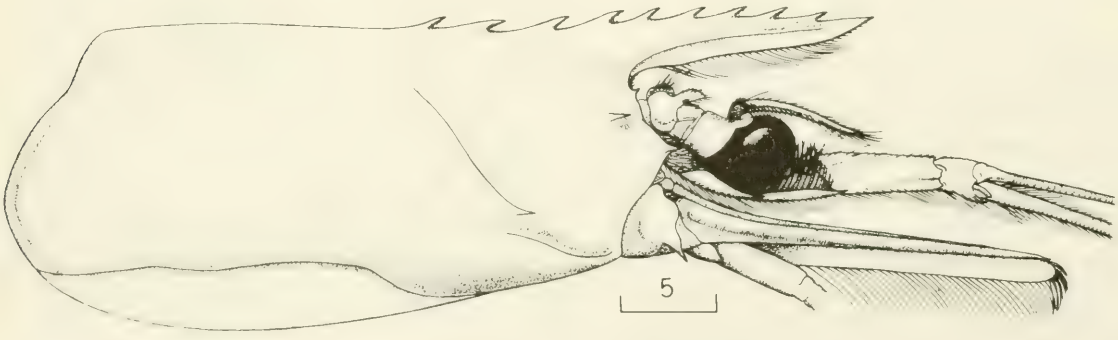

FIGURE 37.—*Pleoticus muelleri*, ♀ 27.5 mm cl, off Laguna Rocha, Uruguay. Cephalothorax, lateral view.

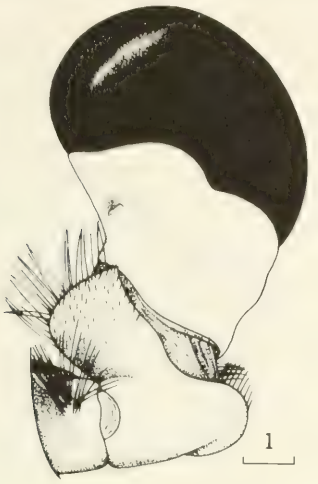

FIGURE 38.—*Pleoticus muelleri*, ♀ 33 mm cl, north of Cabo Santa María, Uruguay. Eye.

dorsal and ventral flagella to that of carapace 2.90 and 2.25 respectively and in shrimp 30 mm cl, 2.5 and 2.0. Scaphocerite exceeding antennular peduncle by 0.2 to 0.3 its own length; lateral rib ending in long spine falling short of distal margin of lamella; antennal flagellum almost 3 times total length of shrimp. Third maxilliped reaching almost to distal margin of third antennular article or surpassing it by as much as 0.5 length of dactyl.

First pereopod reaching between proximal 0.3 and distal margin of carpocerite. Second pereopod overreaching antennular peduncle by almost length of dactyl or by entire propodus. Third pereopod surpassing antennular peduncle by at least length of dactyl and, at most, by propodus and 0.15 length of carpus. Fourth pereopod exceeding carpocerite by as much as entire length of dactyl. Fifth pereopod, longest of all appendages, exceeding antennular peduncle by length of dactyl and 0.15 or 0.20 length of propodus. Order of pereopods in terms of their maximal anterior extensions: first, fourth, second, third, and fifth. First pereopod with spine at midlength of mesial border of basis very long and sharp, and spine on ischium sharp, but smaller than that on basis; second pereopod with setose, squamiform tubercle on distoventral border of coxa, and with long sharp spine on basis. In females, coxa of fifth pereopod produced as rounded, posteromesially directed plate, terminating in tooth anteriorly, plate hinging on horn of posterior plate of sternite XIV; coxa of fourth pereopod narrow, thick, with two rounded mesial projections, base of posterior one hinging on anterior horn of median plate of sternite XIII; coxa of third pereopod produced mesially in subtrapezoidal plate provided with long mesial setae overlapping those of opposite plate, coxa bearing gonopore on dorsomesial surface. In males, coxa of fifth pereopod with large tooth on anterior margin.

Abdomen with middorsal carina along entire length, carina low and rounded from first to third somites (imperceptible in young), and keellike posteriorly; posterodorsal margins of third through fifth somites with median incision; sixth bearing small, sharp spine at posterior end of carina, and small posteroventral spines. Telson with median sulcus moderately deep anteriorly, posteriorly bearing median elevation merging into convex terminal portion; lateral spines moderately long; length of terminal portion about 4 times width at base. Mesial ramus of uropod surpassing apex of telson by 0.15-0.25 of its own length; lateral ramus slightly overreaching mesial ramus and bearing small, terminal distolateral spine.

Petasma (Figure 39*A, B*) cincinnulate along proximal 0.4 of median line; distal part of ventromedian lobule cornified, forming plate bearing terminal suboval projection and lateral spurlike projection; much of lateral lobe heavily sclerotized, overlapping ventral costa, and with shallow lateral emargination marking base of distal portion; latter flexible, subelliptical, directed toward, and partly covered (dorsally) by, ventromedian lobule; ventral costa bearing membranous flap, broadening distally and terminating in paired unequal convexities; free terminal part of costa forming dorsally directed, strongly curved, sharp projection.

Appendix masculina (Figure 39*C, D*) elongate, with heavily sclerotized dorsolateral portion and flexible, subelliptical mesial portion. Appendix interna spatulate, embracing ventromesial margin of appendix masculina proximally, and bearing distolateral tuft of rigid, long setae. Basal sclerite with deep distolateral groove along base of sharp dorsal ridge; ventrolateral spur relatively short.

Thelycum (Figure 40) microscopically setose-punctate, with posterior plate on sternite XIV often divided by median longitudinal groove, and bearing lateral elevations terminating anteriorly in small knob; short anterior part of sternite XIV heavily sclerotized, forming slightly convex,

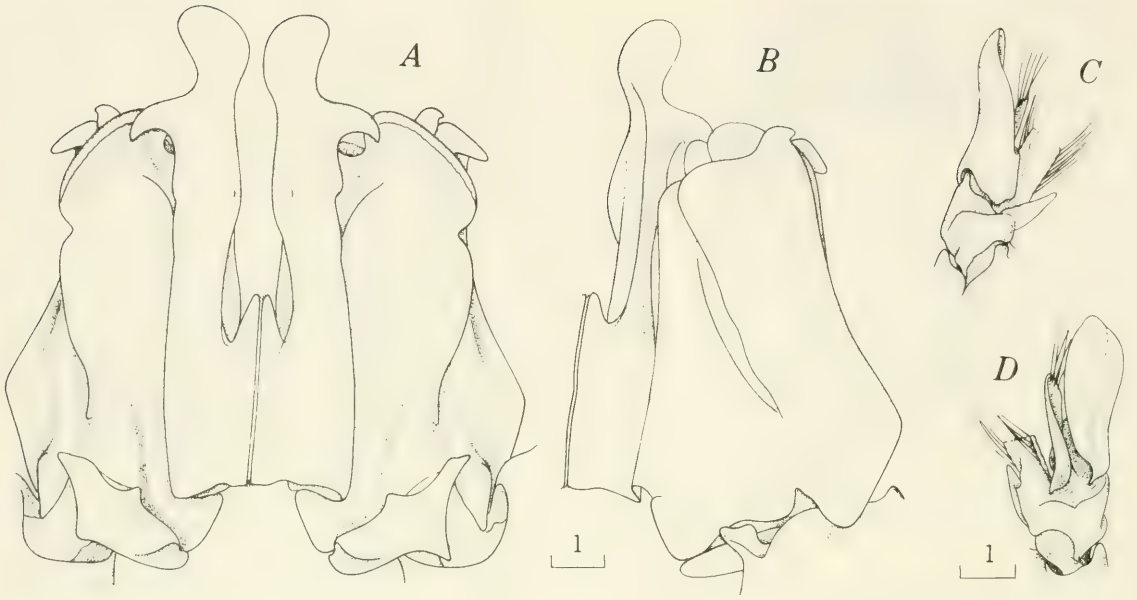

FIGURE 39.—*Pleoticus muelleri*, ♂ 20 mm cl, off Laguna Rocha, Uruguay. *A*, Petasma, dorsal view. *B*, Ventrolateral view of left half. *C*, Right appendices masculina and interna, lateral view. *D*, Mesial view.

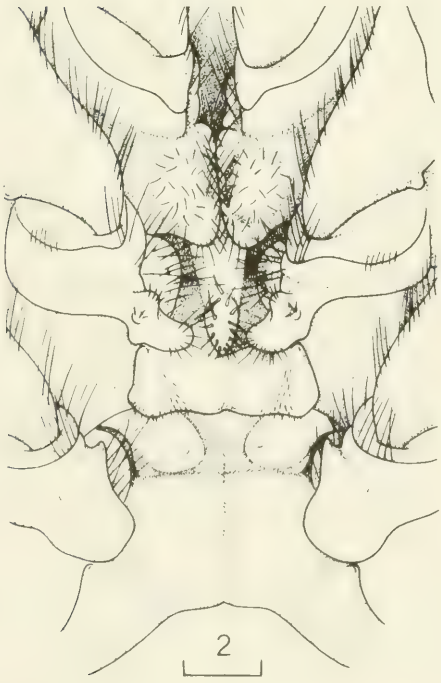

FIGURE 40.—*Pleoticus muelleri*, ♀ 43 mm cl, off Praia de Santana, Espírito Santo, Brazil. Thelycum, ventral view.

paired plates, each bearing pair of minute tubercles. Median plate of sternite XIII elevated laterally in ribs ending anteriorly in blunt horns, and armed with strong, blunt, setose median projection; latter flanked anteriorly by setose protuberances borne on articular membranes of fourth pereopods; sternite XII markedly convex, its strong transverse marginal ridge with deep median depression and blunt, lateral, posteriorly directed horns.

Color.–Pale yellow or yellowish red to tomato red (Boschi and Angelescu 1962); reddish orange of various shades in different areas of the body (Boschi 1963); wine-red in young from 50 mm tl through adulthood (Iwai 1973).

Maximum size.–Males: 37.5 mm cl; females: 58 mm cl.

Geographic and bathymetric ranges.–From off Praia de Santana, about 20°S, 40°W, Espírito Santo (data on label accompanying two specimens collected by Getulio de Souza Neiva), south to the northwestern portion of the Golfo de San Jorge, Comodoro Rivadavia (Figure 34). It occurs most

abundantly in littoral waters at depths between 2 and 20-30 m (Figure 9), and rarely as deep as 80-100 m (Angelescu and Boschi 1960; Boschi and Scelzo 1969a), and from near the shoreline to 0.5 km offshore, occasionally as far as 56 km (Angelescu and Boschi 1960). This species was reported by Iwai (1973) to range north to 21°36′S, the first record north of Ilha Santana, 22°25′S, Rio de Janeiro, where da Silva (1965) had reported a fishery for this shrimp. The specimens taken at Praia de Santana, Espírito Santo, about 178 km north of the locality where Iwai recorded the species, have confirmed the presence of *H. muelleri* beyond the state of Rio de Janeiro. The southernmost limit of the species given above is based on Boschi and Scelzo (1969a), who identified a number of large specimens caught in the Golfo de San Jorge at a depth of 80 m.

Affinities.–*Pleoticus muelleri* has its closest affinities with its Atlantic congener *P. robustus,* but it may be readily separated from it by its almost entirely glabrous body, long prosartema, which may overreach the midlength of the second antennular article, the absence of branchiostegal spines and the presence of orbital spines. Also it may be distinguished by the disposition of the submarginal carina, the posterior part of which is horizontal and situated far from the free ventral border of the carapace, instead of extending subparallel to that border as it does in all other species of this generic complex. The external genitalia of the two are also markedly different, as pointed out under *P. robustus.* In the petasma of *P. muelleri* the ventromedian lobule is cornified distally, terminates in a rounded to ovate platelike projection which bears at its base a spurlike projection, and the ventral costa is produced into a dorsally directed hook. The thelycum, in turn, exhibits paired short plates on the anterior part of sternite XIV, each bearing a pair of minute knobs, and also an exceedingly strong projection on the median plate of sternite XIII.

Spermatophore.–Compound spermatophore (Figure 41) consisting of broad geminate body with angular hump at about midlength, and bearing small pair of wings anterolaterally; also provided with large, highly sculptured midlateral flaps, and pair of broad, posterolateral flanges. Thick, opaque ventral wall of each spermatophore (Figure 42*A*) truncate, lacking anterior lobe, broadened and swollen at about midlength forming hump; area posterior to hump dorsally depressed, and strengthened by longitudinal ridge. Lateral wall mostly thick, concave, and insensibly continuous with wing anteriorly, merging with broad, subrectangular flap, and posteriorly bearing prominent longitudinal ridge parallel to that of ventral wall. Dorsomesial wall largely translucent, but heavily sclerotized and opaque mesially forming axial part of complex armature (Figure 42*C*). Latter bearing three transverse ribs: 1) anterior, forming arc, with one arm (ventral) strengthening ventral hump and another running across dorsomesial wall, then ending in foliaceous process; 2) intermediate, close to former, very strong, tonguelike, and deeply excavated; 3) posterior, forming shelf projecting inside lumen of sperm sac from dorsomesial wall. Wing short, broad, and flexible except for posterior thickening running along its entire length. Anterior part of flap broad, subrectangular, elevated in marginal

FIGURE 41.—*Pleoticus muelleri.* Compound spermatophore attached to female, ♀ 37 mm cl, Rawson, Chubut, Argentina (setae omitted).

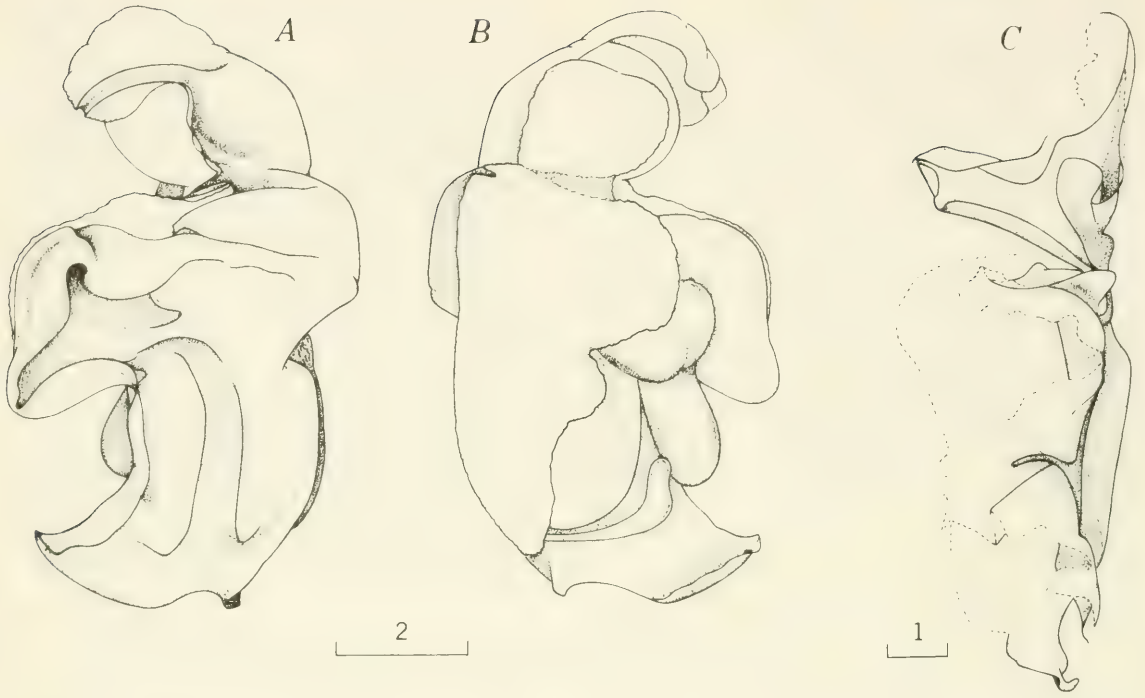

FIGURE 42.—*Pleoticus muelleri*, ♂ 37 mm cl, off Buenos Aires Province, Argentina. *A*, Right spermatophore dissected from terminal ampulla, ventrolateral view. *B*, Dorsomesial view. *C*, Left spermatophore dislodged from female, ♀ 59 mm cl, Puerto Madryn, Chubut, Argentina.

ridge continuous with hump; posterior part narrow, extending as flexible band joining flange. Flange short, with broad mesial base and sinuous lateral margin. Dorsal plate (Figure 42*B*) large, extending almost from anterior extremity of spermatophore to base of flange, and irregular in contour.

Compound spermatophore applied to thelycum much as it is in *P. robustus*. Anterior extremity of geminate body lying opposite female gonopores, with wings attached to ventral articular membranes of third pereopods. Ventral walls fused mesially while lateral walls diverge dorsally becoming affixed to sternite XIII, their lateral margins embracing mesial prominences of dorsal articular membranes of fourth pereopods. Strong humplike prominences projecting ventrally from sternite XIV, latter serving as place of attachment for broad anterior parts of flaps as well as for intimately fused dorsal plates. From humplike prominences, compound spermatophore sloping posterodorsally, and held in position by paired flanges affixed to ventral articular membranes of fifth pereopods.

The sperm is freed from each sac through an anterior rupture of dorsomesial wall, close to corresponding gonopores. The gelatinous substance which accompanies the sperm within the sperm sac may be observed covering the gonopores in Figure 41. Spermatophore-bearing females are not infrequent in collections; it seems that the spermatophores in this species as in *P. robustus*, which are also exceedingly large, become firmly anchored to the thelycum. According to Angelescu and Boschi (1960), the spermatophores in recently caught impregnated females are light green.

Postembryonic stages.–Boschi and Scelzo (1969a) prepared illustrated keys for the identification of larvae of the three more common Penaeidea in the waters off Argentina. These keys include diagnoses of protozoeae, mysis, and postlarvae of *P. muelleri* based both on specimens caught in plankton samples and others reared in the laboratory. Later, Scelzo and Boschi (1975) presented the results of their successful rearing of this shrimp from eggs spawned in the laboratory to

juveniles of an average total length of 21.3 mm. They stated that spawning generally took place the night following the capture of mature females, and eggs hatched between 12 and 24 h (according to the temperature) after being released. The young passed through 6 nauplii, 3 protozoeae, 3 mysis, and an undetermined number of postlarvae before becoming juveniles. The larval development was completed in 19-23 days at 19.0°-23.5°C and juveniles reached 21.3 mm (average) in 81 days after hatching. In more recent experiments, Boschi and Scelzo (1976) found that, at 24°C, *P. muelleri* attained an average of 61 mm tl and 2.7 g in 180 days after hatching. The studies mentioned above are the only ones that have been made on the development of any of the 12 species treated here.

Remarks.–Much of our knowledge of the morphology of this species is due to the study of Angelescu and Boschi (1960) and their subsequent contribution (Boschi and Angelescu 1962). These authors presented detailed accounts of the external and internal anatomy, and included outlines and a brief description of the "green" spermatophores on the female. In addition, they calculated the rate of growth of the species in Argentinian waters, studied the development of the testis and ovaries, and determined that the spawning season there extends from December to February (i.e., through the summer months). Furthermore, they found that it feeds on organic detritus as well as on small animals, such as sergestids and polychaetes, and plants.

Ecological notes.–Pleoticus muelleri is the only species of the genus which frequents shallow littoral waters; it even invades seawater channels and rías like those in the vicinity of Bahía Blanca, Buenos Aires, where, according to Boschi (1963), the "langostino" is trapped in weirs by the fishermen. Furthermore, this shrimp not only inhabits such shallow waters, but occurs in sufficient abundance to support commercial exploitation in many areas.

This species completes its entire life cycle in the sea but, as stated above, may frequent inshore waters of high salinity. It occupies tropical and subtropical waters off Brazil, where surface temperatures are as high as 25°-27°C during the warm months of the year, and 16°-17°C during the cold ones; farther south, off Argentina, it occurs in temperate waters where surface temperatures range between 10° and 23°C during the summer, and 5° and 10°C during the winter (Boschi 1964).

This shrimp lives on mud and sand bottoms.

Economic importance.–Pleoticus muelleri is taken commercially from Ilha Santana, Rio de Janeiro, to Punta Clara, Chubut. Significant catches, however, are made only from Santa Catarina to Punta Clara, and the largest fisheries are in Argentinian waters (Boschi 1964), between Punta Rasa (province of Buenos Aires) and Punta Clara, i.e., between 41° and 44°S. This species constitutes the largest percentage of the shrimp landings (which also include *Artemesia longinaris* Bate 1888) in Argentina.

Hadropenaeus New Genus

Hymenopenaeus. Smith 1885:179 [part]. Burkenroad 1936:102 [part]. Kubo 1949:212 [part].
Philonicus Bate 1888:273 [part].
Pleoticus Bate 1888:xii [part].
Haliporus. Bouvier 1906b:1 [part]; 1908:78 [part]. A. Milne Edwards and Bouvier 1909:206 [part]. de Man 1911:31 [part].

Diagnosis.–Body stout, carapace proportionately short, integument moderately thick, firm. Rostrum short, not overreaching distal margin of first antennular article, deep, ventral margin pronouncedly convex; armed only with dorsal teeth; epigastric tooth and first rostral separated by interval equal to, or only slightly greater than, that between first and second rostral teeth. Orbital and pterygostomian spines absent; postorbital, antennal, hepatic, and branchiostegal spines present. Cervical sulcus long, almost reaching middorsum of carapace; hepatic sulcus deep; branchiocardiac sulcus and carina absent, posthepatic and submarginal carinae absent. Abdomen carinate dorsally from third through sixth somites. Telson with pair of conspicuous, fixed, lateral spines. Prosartema long, flexible. Antennular flagella longer than carapace, usually subcylindrical, ventral flagellum occasionally depressed. Mandibular palp two jointed, articles moderately broad, distal one as long as or slightly shorter than basal, and tapering to blunt apex. First maxilla with unsegmented palp (endite of basis) gently narrowing to rounded apex. Fifth pereopod subflagelliform and considerably longer than fourth. First pereopod with spine on basis,

ischium, and merus. Exopods on all maxillipeds and pereopods. Lateral ramus of uropod armed with distolateral spine reaching distal margin of lamella (terminal spine). In males, petasma with ventral costa free from heavily sclerotized, platelike terminal part of ventrolateral lobule; ventromedian lobule broadly expanded distally. Endopod of second pereopod bearing appendices masculina and interna, and with basal sclerite produced distally into elongate ventrolateral spur. Thelycum of open type, not enclosing seminal receptacle. Pleurobranchia on somites IX to XIV; single rudimentary arthrobranchia on VII, and anterior and posterior arthrobranchiae on somites VIII to XIII; podobranchia on second maxilliped, and epipod on second maxilliped (and on first if proximal exite of coxa considered an epipod) through fourth pereopod.

Hadropenaeus is an extremely homogeneous genus, the three known species being quite similar.

Type-species.–*Hymenopenaeus modestus* Smith 1885.

Etymology.–From the Greek *hadros,* stout, in combination with the generic name *Penaeus,* alluding to the comparatively short and thick carapace.

Gender.–Masculine.

List of species.–Amphi-Atlantic: *Hadropenaeus affinis* (Bouvier 1906b). Western Atlantic: *Hadropenaeus modestus* (Smith 1885). Indo-West Pacific: *Hadropenaeus lucasii* (Bate 1881).

Affinities.–The members of *Hadropenaeus* resemble those of *Pleoticus* (as here defined) in having the epigastric tooth separated from the first rostral by an interval equal to, or only slightly greater than, that between the first and second rostral teeth, in lacking both branchiocardiac and posthepatic carinae, and in possessing a petasma in which the ventral costa is free from the platelike, terminal part of the ventrolateral lobule. However, *Hadropenaeus* differs from *Pleoticus* (as well as from the other closely related genera except *Mesopenaeus*) in the proportionately higher carapace, in the shape of the rostrum which is short, deep, and possesses a strongly convex ventral margin, and in lacking submarginal carinae.

The members of this genus are closely allied to those of *Mesopenaeus.* They share a stout appearance, short, deep rostrum in which the ventral margin is convex, similar arrangement of the epigastric and rostral teeth, and they lack branchiocardiac sulci and carinae. Furthermore, the ventral flagellum, which is typically flattened in *Mesopenaeus,* is occasionally depressed in one species of *Hadropenaeus;* the depressed flagellum seemingly represents the first step in a process of specialization which progressed through the flattened ventral flagellum in *Mesopenaeus,* and culminated in the two lamellate flagella (both ventral and dorsal) in *Solenocera. Hadropenaeus,* in contrast to *Mesopenaeus,* lacks submarginal carinae and orbital spines; it possesses branchiostegal spines and, most significantly, exhibits a petasma in which the ventral costa is free from the terminal part of the ventrolateral lobule.

Key to Species of *Hadropenaeus*

1. Rostrum lacking conspicuous carina dorsal to adrostral one. Thelycum with median protuberance on sternite XIV high, projecting ventrally as far as posterior convexities of sternite XIII; latter with median ridge bearing large tooth anteriorly. Petasma with ventromedian lobule produced into distolateral projection 2

   Rostrum with conspicuous carina dorsal to adrostral one. Thelycum with median protuberance on sternite XIV low, not projecting ventrally as far as posterior convexities of sternite XIII; latter with median, keellike ridge lacking tooth anteriorly. Petasma with ventromedian lobule not produced into distolateral projection .... *H. lucasii*

2. Scaphocerite reaching distal end of antennular peduncle or overreaching it by not more than 0.1 of its own length. Prosartema extending only to distomesial extremity of first antennular article. Thelycum with median protuberance on sternite XIV projecting ventrally, and tooth of median keel of sternite XIII directed anteriorly. Petasma with distomesial projection of

ventromedian lobule directed mesially ..... *H. affinis*

Scaphocerite overreaching antennular peduncle by about 0.25 of its own length. Prosartema conspicuously overreaching distomesial margin of first antennular article. Thelycum with median protuberance on sternite XIV projecting anteriorly, and tooth of median keel of sternite XIII directed ventrally or posteriorly. Petasma with distomesial projection of ventromedian lobule directed distally .... *H. modestus*

Hadropenaeus affinis (Bouvier 1906)

Figures 9, 43, 44A, 45-49

Haliporus modestus Bouvier 1905a:980. [Not *Hymenopenaeus modestus* Smith 1885.]

Haliporus affinis Bouvier 1906b:4 [syntypes: 1 ♂ 2 ♀, 4 ♂ 4 ♀, 2 ♂ 2 ♀, MP; type-locality: off Cape Verde Is, 16°53′N, 25°10′W, 410-460 m, 29 July 1883, *Talisman* stn 116. Unrecorded number of syntypes from off Cape Verde Is, "100 m" from uncited *Talisman* station. 1 ♂, MCZ 7196, off Barbados, 188 m, 5 March 1879, *Blake* stn 273, 13°03′05″N, 59°36′18″W]. Bouvier 1908:80. A. Milne Edwards and Bouvier 1909:209. de Man 1911:7.

Hymenopenaeus affinis. Burkenroad 1936:104. Crosnier and Forest 1973:258, fig. 82b, 84, 94d.

Hymenopenaeus modestus. Bullis and Thompson 1965:5 [part]. [Not *Hymenopenaeus modestus* Smith 1885.]

Material

UNITED STATES—North Carolina: 2 ♀, UNC-IMS, SE of Cape Lookout, 229 m, 8 June 1949, *Albatross III* stn 21-4. 3 ♂ 14 ♀, USNM, E of Port Fisher, 366 m, 15 November 1956, *Combat* stn 177. 2 ♂ 1 ♀, UNC-IMS, about 111 km SE of Cape Fear, 412-369 m, 23 June 1956, *Pelican* stn 75. South Carolina: 2 ♀, USNM, E of Cape I, 366 m, 20 April 1957, *Combat* stn 288. Florida: 1 ♀, USNM, off Hobe Sound, 302-285 m, 21 May 1968, *Gerda* stn 997. 1 ♀, USNM, off Boca Raton, 366 m, 29 March 1956, *Pelican* stn 17. 1 ♂, USNM, SE of Key Largo, 185 m, 22 January 1965, *Gerda* stn 452. 1 ♂, USNM, off Marathon, 201 m, 21 June 1967, *Gerda* stn 813. 1 ♂, USNM, S of Pine Is, 293-302 m, 25 February 1969, *Gerda* stn 1029. 2 ♀, USNM, NW of Double Headed Shot Cays, 223 m, 29 August 1967, *Gerda* stn 864. 1 ♂, USNM, NW of Charlotte Harbor, 366 m, 21 August 1970, *Oregon II* stn 11180.

BAHAMA ISLANDS—1 ♂, RMNH, NW of Matanilla Reef, 549-567 m, 1 July 1963, *Gerda* stn 179. 1 ♂, USNM, NW of Matanilla Reef, 466-417 m, 30 September 1967, *Gerda* stn 935. 1 ♀, USNM, NW of Matanilla Reef, 421 m, 3 February 1957, *Combat* stn 238. 1 ♀, USNM, N of Matanilla Reef, 393 m, 3 February 1957, *Combat* stn 237. 2 ♂, RMNH, W of Bimini Is, 452-474 m, 30 January 1964, *Gerda* stn 234. 3 ♀, USNM, SW of Bimini Is, 403-421 m, 30 January 1964, *Gerda* stn 233. 5 ♀, RMNH, off Gun Cay, 439-421 m, 29/30 January 1964, *Gerda* stn 232. 1 ♂, USNM, SW of Gun Cay, 312-348 m, 30 March 1964, *Gerda* stn 274. 1 ♂ 1 ♀, USNM, Santaren Channel, 384-366 m, 6 November 1960, *Silver Bay* stn 2468. 1 ♀, USNM, Santaren Channel, 412-220 m, 22 June 1967, *Gerda* stn 820. 1 ♀, USNM, S of Great Inagua, 311 m, 13 December 1969, *Oregon II* stn 10849.

PUERTO RICO—3 ♀, USNM, Mona Passage, 366 m, 17 October 1963, *Silver Bay* stn 5190.

HAITI—1 ♀ juv, USNM, W of Anse d'Hainault, [?] 77 m, 2 July 1970, *Pillsbury* stn 1186.

LESSER ANTILLES—1 ♂, USNM, E of Rivière Pilote, Martinique I, 170-214 m, 9 July 1969, *Pillsbury* stn 907. 1 ♂, USNM, SE of Georgetown, St Vincent I, 165-201 m, 6 July 1969, *Pillsbury* stn 874. 1 ♂ syntype + 1 ♂, MCZ 7196, off South Point, Barbados, 188 m, 5 March 1879, *Blake* stn 273.

WESTERN CARIBBEAN—2 ♂ 4 ♀, USNM, Arrowsmith Bank, 311-146 m, 28 January 1968, *Gerda* stn 954. 1 ♀, USNM, Arrowsmith Bank, 307-192 m, 28 January 1968, *Gerda* stn 951. 1 ♂, UMML, Arrowsmith Bank, 252-293 m, 14 March 1968, *Pillsbury* stn 591. 2 ♂ 2 ♀, USNM, Arrowsmith Bank, 155-205 m, 15 March 1968, *Pillsbury* stn 598. 1 ♂, USNM, W of I de Providencia, 289-274 m, 4 February 1967, *Oregon* stn 6423.

MEXICO—Quintana Roo: 1 ♂ juv, UMML, SE of Isla Mujeres, 241-320 m, 10 September 1967, *Gerda* stn 893. 1 ♀, UMML, SE of Isla Mujeres, 210-366 m, 23 August 1970, *Gerda* stn 1286. 3 ♀, USNM, off Puerto de Morelos, 165-168 m, 10 September 1967, *Gerda* stn 899.

PANAMA—1 ♀, USNM, off Caribbean coast of Panama, 274 m, 5 July 1972, *Canopus*.

PORTUGAL—Cape Verde Is: 1 ♂ 2 ♀, 4 ♂ 4 ♀, 2 ♂ 2 ♀ syntypes, MP, 410-460 m, 29 July 1963, *Talisman* stn 116.

Description.–Body stout (Figure 43), integument moderately thick, firm. Carapace with restricted pubescent areas, setae dense and long at base of rostrum, on pterygostomian region, and in patch extending from orbital margin to epigastric tooth; minute, sparsely set setae on dorsum and hepatic region. Abdomen polished, almost entirely naked except for setae on posterior part of dorsal keel; telson and mesial ramus of uropod rather densely pubescent. Rostrum short, its length 0.20-0.25 that of carapace, falling short of distal margin of first antennular article, almost horizontal, with dorsal margin straight and ventral margin strongly convex, with subapical concavity giving rise to saber-shaped tip; latter almost 0.4 length of rostrum. Rostral plus epigastric teeth 5-7 (mode 6; $N = 60$), base of third rostral tooth at level of orbital margin. Adrostral carina extending from orbital margin to ultimate tooth; more dorsal barely perceptible carina extending from second to ultimate rostral tooth; postrostral

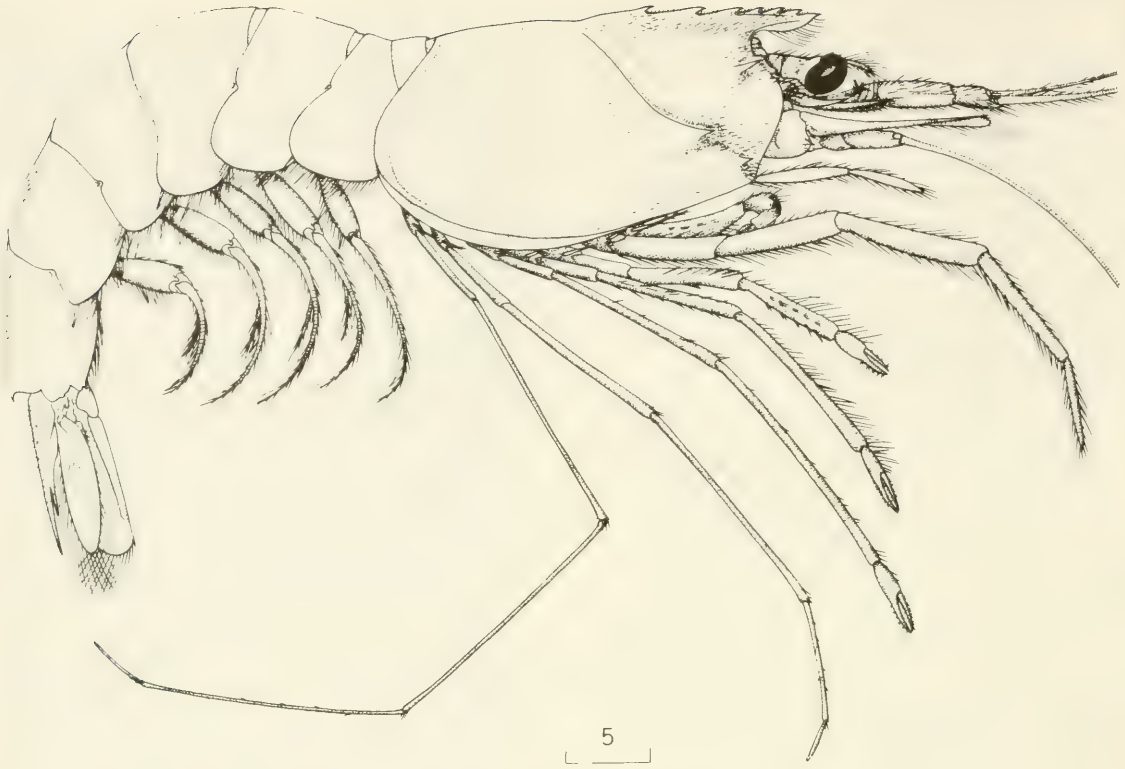

FIGURE 43.—*Hadropenaeus affinis*, ♀ 21.5 mm cl, Mona Passage, off Puerto Rico. Lateral view (third pereopod slightly raised).

carina ending immediately posterior to cervical sulcus. Orbital margin produced anteriorly into ventrally inclined, short shelf. Postorbital spine, longest of four lateral spines on carapace, located dorsal to base of small antennal spine; branchiostegal and hepatic spines sharp. Cervical sulcus deep, ending dorsally just posterior to midlength of carapace, and close to postrostral carina; cervical carina sharp; hepatic sulcus subhorizontal posteriorly, inclined anteroventrally from depressed area below hepatic spine to pit below branchiostegal spine.

Eye (Figure 44*A*) with basal article produced distomesially into pubescent, elongate scale; ocular peduncle moderately long, bearing minute tubercle; cornea broad, greatest diameter 1.5-1.9 times that of base of ocular peduncle, strongly slanting posterolaterally.

Antennular peduncle length equivalent to 0.65 that of carapace; prosartema falling short, or barely reaching, distomesial margin of first article; stylocerite length about 0.65 of distance between lateral base of first article and base of distolateral spine, terminating in sharp spine; distolateral spine very slender and long, conspicuously surpassing proximal margin of second article. Antennular flagella long, length of dorsal flagellum 2.2 and 1.9 times carapace length in shrimp 8 and 23 mm cl, respectively; ventral shorter and broader than dorsal, gently tapering distally, and armed with marginal rows of long plumose setae. Scaphocerite extending to distal margin of antennular peduncle or exceeding it by less than 0.1 of its own length; lateral rib ending in slender spine, reaching to or very slightly beyond distal margin of lamella. Antennal flagellum long, although incomplete in all specimens examined, longest observed by me 3 times total length of shrimp. Mandibular palp (Figure 45*A*) moderately broad, distal article slightly shorter than basal. First maxilliped as illustrated (Figure 45*B*); rudimentary arthrobranchia of corresponding somite VII situated near its base (Figure 45*c*-*c*^{1}). Third maxilliped exceeding antennular peduncle by length of dactyl and half or as much as entire length of propodus.

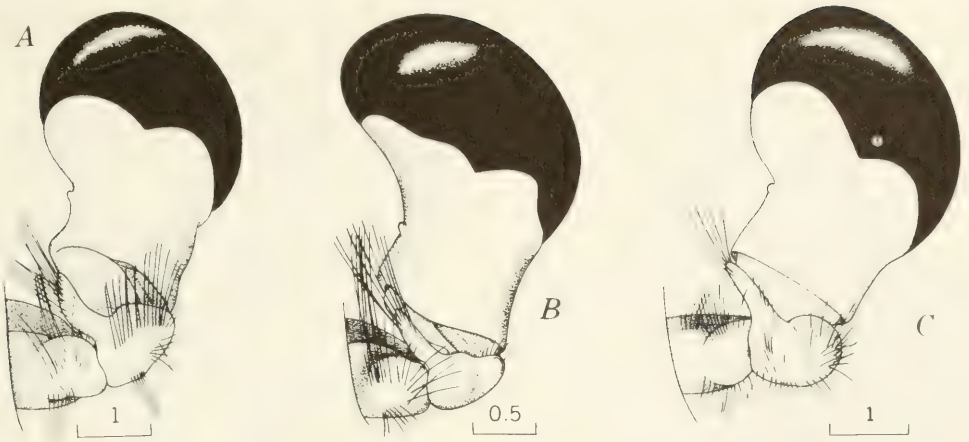

FIGURE 44.—Eyes. *A*, *Hadropenaeus affinis*, ♀ 21 mm cl, southeast of Cape Lookout, N.C. *B*, *Hadropenaeus modestus*, ♂ 11 mm cl, southwest of Dry Tortugas, Fla. *C*, *Hadropenaeus lucasii*, ♀ 18 mm cl, Pailolo Channel, Hawaiian Islands.

First pereopod, stoutest of all, reaching at least basal 0.65 length of carpocerite, and, at most, exceeding it by tip of dactyl. Second pereopod moderately stout, extending to distal end of carpocerite or exceeding it by as much as entire propodus. Third pereopod surpassing antennular peduncle by length of dactyl or by entire propodus. Fourth pereopod exceeding antennular peduncle by dactyl and 0.2-0.6 length of propodus; length of dactyl about 0.4 that of propodus; length of carpus about 1.25 times that of merus. Fifth pereopod slender and long, overreaching antennular peduncle at least by length of dactyl and propodus, or by as much as their length and almost 0.3 length of carpus. Order of pereopods in terms of their maximal anterior extensions: first, second, fourth, third (occasionally third, fourth), and fifth. First pereopod with very long, slender spine on basis, small spine on distomesial margin of ischium, and small one near midlength of mesial margin of merus. Second pereopod with long spine on basis. Coxa of fourth and fifth pereopods in males armed with anterior spine. Coxa of fifth pereopod in females produced mesially into short plate bearing sharp spine anteromesially.

Abdomen with middorsal keel from fourth through sixth somites; low rounded carina sometimes present on third; posterodorsal margin of third, fourth, and fifth somites with median incision; sixth somite bearing sharp spine at pos-

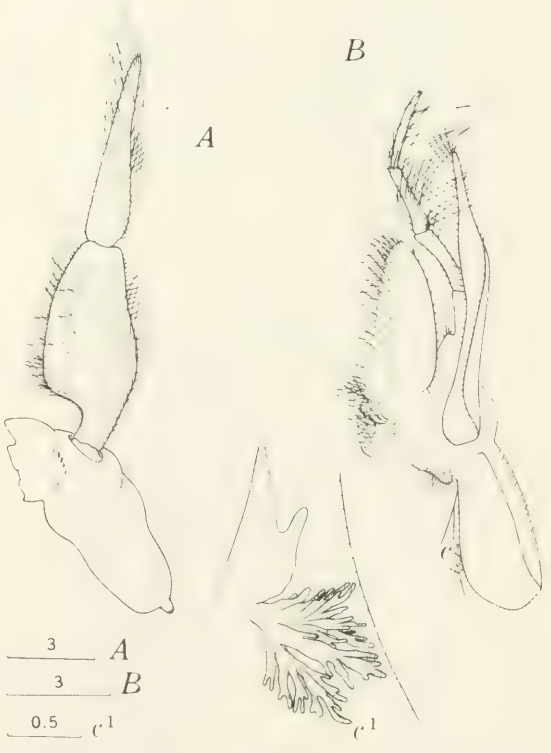

FIGURE 45.—*Hadropenaeus affinis*, ♀ 21.5 mm cl, southeast of Cape Lookout, N.C. *A*, Mandible. *B*, First maxilliped. *c*, Arthrobranchia. c^1, Enlargement of *c* (all from left side).

terior end of keel, and minute spine at posteroventral angles. Telson (Figure 46*A*) pubescent except for median sulcus and terminal portion; sulcus deep anteriorly, increasingly shallow posteriorly, ending before reaching lateral spines; spines long, their length 1.6-1.9 basal width of terminal portion; latter long, length 3.5-4.5 times basal width; mesial ramus of uropod barely overreaching apex of telson, or exceeding it by about 0.15 of its own length; lateral ramus distinctly surpassing mesial, and armed with small, distolateral spine, projecting beyond contiguous distal margin of ramus.

Petasma (Figure 47*A, B*) cincinnulate along proximal 0.65 of median line; broad distal part of ventromedian lobule strongly produced into elongate, distally directed distomesial projection, and short distolateral projection; entire terminal margin of lobule spinulous; distal part of ventrolateral lobule heavily sclerotized, forming plate, with border adjacent to ventral costa bearing emargination delimiting basal part from subovate terminal part; latter strongly inclined toward, and partially covered by, ventromedian lobule, and armed with minute spinules along ventral margin; ventral costa with distal part free from contiguous plate, bent outward and bearing spinules on distalmost margin.

Appendix masculina (Figure 47*C, D*) with proximal part broad, strongly produced mesially into thickened lobe, and bearing long setae along lateral margin; distal part narrow, strongly turned laterally, with apical portion armed with tuft of long setae; appendix interna shorter than appendix masculina, narrow, sinuous, and bearing apical tuft of long setae. Ventrolateral spur large, subelliptical to paddlelike.

Thelycum (Figure 48*A, B*) with median protuberance on sternite XIV subconical, its apical portion directed anteriorly or ventrally and produced into spinelike projection; protuberance situated distinctly posterior to prominent, setose, paired convexities of posteriormost part of sternite XIII; longitudinal median keel on sternite XIII produced anteriorly into anteriorly directed blunt tooth, its cephalic margin concave, its posterior margin convex.

FIGURE 46.—Telsons. *A*, *Hadropenaeus affinis*, ♀ 20 mm cl, southwest of Bimini Islands, Great Bahama Bank. *B*, *Hadropenaeus modestus*, ♀ 19 mm cl, west of Isla de Providencia, western Caribbean.

Photophores.–Paired photophores situated on posterolateral margins of sternites X through XIII just mesial to coxae of first four pairs of pereopods.

Color.–Color notes made by Lipke B. Holthuis (pers. commun.) on a male caught southeast of Georgetown, St. Vincent Island, at *Pillsbury* stn 874, state that the shrimp was "uniformly red, with darker bands parallel to the posterior margins of the abdominal terga."

The following description is based upon a freshly caught specimen observed by me during a 1969 cruise of *Oregon II,* south of Great Inagua Island, Bahamas. Body translucent pinkish orange, with gnathal appendages, and pereopods reddish orange. Carapace with milky white subtriangular patch lying immediately dorsal to hepatic spine, its broad base abutting cervical sulcus; small, middorsal, diamond shaped marking (formed by white lines) just posterior to midlength of carapace; anterolateral sides of marking continuing posterolaterally in dorsalmost arm of transverse, strongly sinuous, opaque white, narrow band; ventral arm of U-shaped dorsal portion of band extending anteriorly to cervical sulcus,

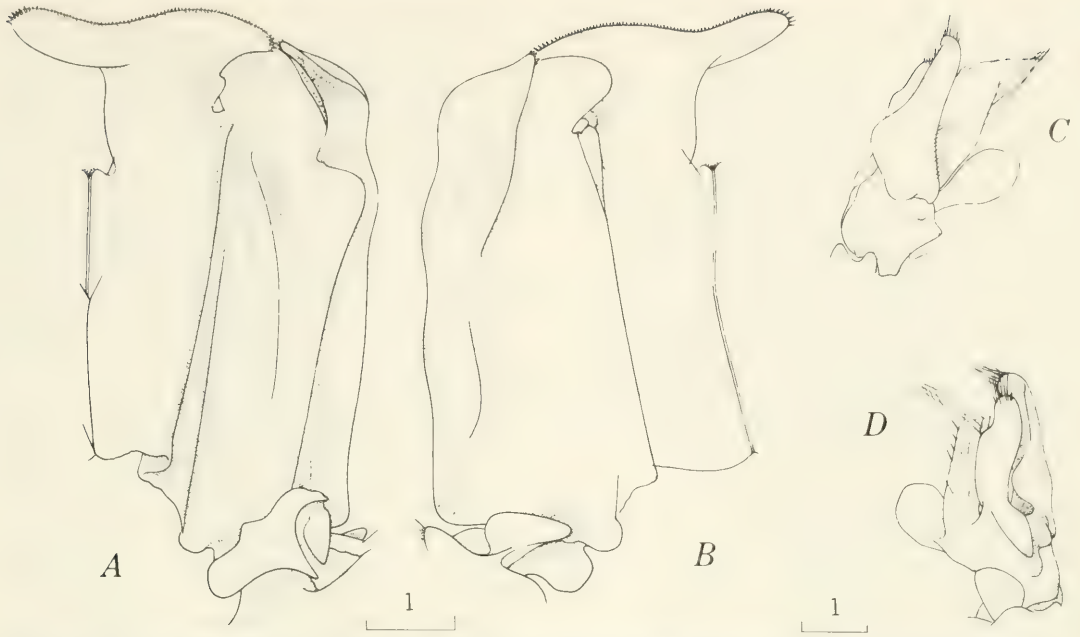

FIGURE 47.—*Hadropenaeus affinis*, ♂ 16 mm cl, about 11 km southeast of Cape Fear, N.C. *A*, Petasma (partly bent laterally), dorsal view of right half. *B*, Ventral view. *C*, Right appendices masculina and interna, dorsal view. *D*, Ventromesial view.

there turning caudad reaching posterior end of hepatic sulcus; middorsal patch of white specks extending from posterior sides of diamond to posterior margin of carapace. First five abdominal somites with reddish orange band along posterior margin of tergum, band broader dorsally, tapering posteroventrally to level of articular knob, then extending anteroventrally to about mid-

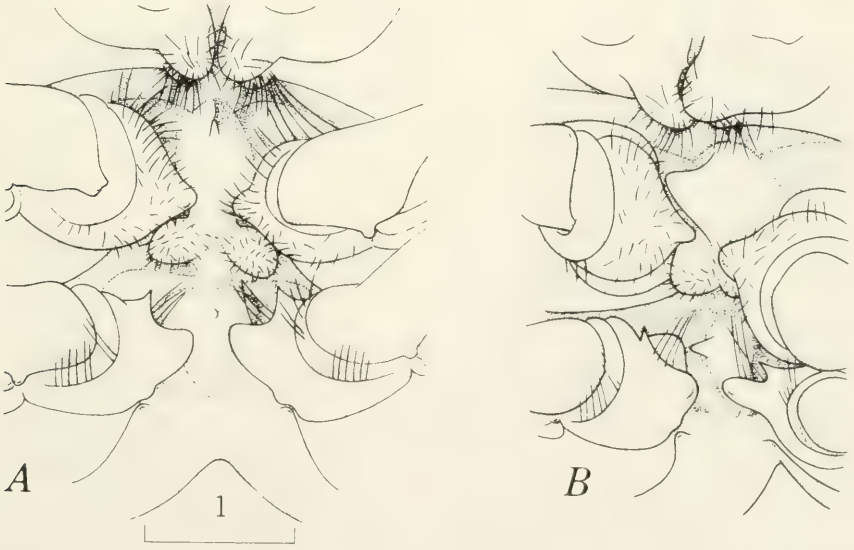

FIGURE 48.—*Hadropenaeus affinis*, ♀ 19 mm cl, east of Cape Island, S.C. *A*, Thelycum, ventral view. *B*, Ventrolateral view.

length of ventral margin of pleuron and from there anteriorly to ventral angle of latter.

Maximum size.–Males: 15 mm cl, about 66 mm tl; females: 23 mm cl, about 82 mm tl.

Geographic and bathymetric ranges.–In the western Atlantic: from off Cape Lookout, N.C. (34°15′N, 75°58′W), southward to the Straits of Florida, in the northeastern part of the Gulf of Mexico (northwest of Charlotte Harbor, Fla.), and throughout the Caribbean. In the eastern Atlantic: off Cape Verde Islands (Figure 49). This species has been found at depths between 165 and 570 m (Figure 9), with one dubious record from Haiti at 77 m.

Affinities.–Hadropenaeus affinis, which is amphi-Atlantic, and *H. modestus,* found only in the western Atlantic, are closely allied, but can be distinguished by the characters presented in Table 1.

Burkenroad (1936), for unexplained reasons, expressed doubt that *H. affinis* is different from *H. modestus,* an opinion apparently shared by Bullis and Thompson (1965) who recognized only *H. modestus* in their western Atlantic collections. I have examined part of their material and found that it also includes *H. affinis.* On the basis of the original description of *H. modestus* (Smith 1885), Bouvier (1906b) distinguished *H. affinis* from the former species by six features. I have found that two of them are diagnostic: the relative length of the scaphocerite, and the ratio length of dactyl/length of propodus of the fourth pereopod (see Table 1). The number of rostral teeth is not 7 in *H. modestus* as Smith indicated, but 6 in all specimens I have examined, the number usually possessed by *H. affinis.* The relative length of the antennular flagella, which Bouvier indicated was greater in *H. affinis,* varies within a given length of carapace, and may be the same in animals of the two species, e.g., 1.9 times carapace length in shrimp 23 mm cl. The carpus of the fourth pereopod is longer than the merus in both species, and not shorter in *H. modestus,* as Bou-

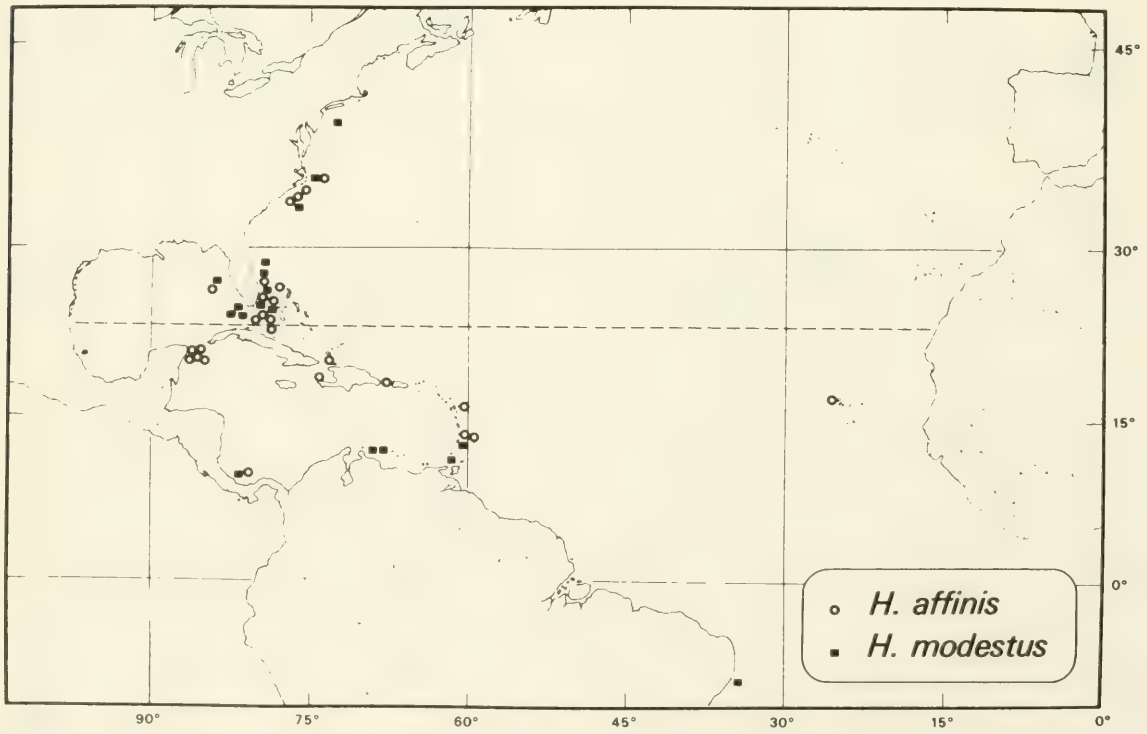

FIGURE 49.—Ranges of *Hadropenaeus affinis* and *Hadropenaeus modestus* based on published records and specimens personally examined.

TABLE 1.—Characteristics distinguishing *Hadropenaeus affinis* from *H. modestus*.

Feature	*H. affinis*	*H. modestus*
Scaphocerite	Reaching distal end of antennular peduncle or surpassing it by less than 0.10 of its own length	Surpassing antennular peduncle by as much as 0.25 of its own length
Prosartema	Extending only to distomesial extremity of first antennular article	Conspicuously overreaching distomesial extremity of first antennular article
Fourth pereopod	Extending farther anteriorly than third pereopod; surpassing antennular peduncle by as much as length of dactyl and that of propodus; length of dactyl less than 0.5 that of propodus	Not extending so far anteriorly as third pereopod, reaching at most distal end of first antennular article; length of dactyl greater than 0.5 that of propodus
Coxa of fifth pereopod in females	Bearing strong anteromesial spine	Lacking anteromesial spine in adult, occasionally with inconspicuous one in juvenile
Terminal portion of telson	Long, length 3.5-4.5 its basal width	Short, length 2.5-3.3 its basal width
Telsonic spines	Long, length more than 1.5 basal width of terminal portion of telson	Short, length not more than basal width of terminal portion of telson
Telsonic pubescence	Extensive, lacking on terminal portion	Limited to paired rows flanking median sulcus and lateral margins
Petasma	Ventromedian lobule with distomesial projection directed mesially; distal part of dorsolateral lobule subelliptical	Ventromedian lobule with distomesial projection directed distally; distal portion of dorsolateral lobule subrectangular
Thelycum	Protuberance of sternite XIV mammiform, with apical part directed ventrally; median keel of sternite XIII produced into anteriorly directed blunt tooth	Protuberance of sternite XIV subovate, with apical part directed anteriorly; median keel of sternite XIII produced into ventrally or posteriorly directed blunt tooth

vier calculated from Smith's erroneous data. Finally, the lateral ramus of the uropod is similar in shape in the two species, its distal part truncate and turning gently proximomesially. The descriptions of both the petasma and the thelycum of *H. affinis* presented by A. Milne Edwards and Bouvier (1909), together with the two diagnostic characters mentioned above, adequately diagnose the species.

Specimens from various localities in the western Atlantic exhibit differences in the shape of coxal spine of the fifth pereopod which varies from nearly blunt to sharply acute. Also in the sculpture of the thelycum, the apical portion of the protuberance on sternite XIV may be directed anteriorly or ventrally. The observed variations, however, intergrade and, furthermore, in some specimens the shape of the spine and the direction of the protuberance are identical to those exhibited by the syntypic material.

Remarks.–The numerous records cited above are the first from the western Atlantic since Bouvier (1906b) cited a syntypic male from off Barbados (*Blake* stn 273) in the original description of the species, and A. Milne Edwards and Bouvier (1909) recorded an additional juvenile male, which had been taken with the syntype.

The presence of photophores on the thoracic sternites of this species is revealed here for the first time. The photophores were observed in a recently caught specimen obtained from the *Oregon II*, south of Great Inagua, Bahamas; they are similar to those described by Burkenroad (1936) in *Hymenopenaeus debilis*.

Hadropenaeus modestus (Smith 1885)

Figures 9, 44B, 46B, 49-52

Hymenopenaeus modestus Smith 1885:183 [holotype: ♀ USNM 7267; type-locality: off Bethany Beach, Del., 38°31'N, 73°21'W, 156 fm (285 m), *Fish Hawk* stn 1047]. Burkenroad 1936:104. Bullis and Thompson 1965:5 [part]. Crosnier and Forest 1973:259.

Haliporus modestus. Bouvier 1905a:980; 1906b:4; 1908:80. A. Milne Edwards and Bouvier 1909: 209. de Man 1911:7. Fowler 1912:543.

Material

UNITED STATES—Delaware: ♀ holotype, USNM 7267, off Bethany Beach, 285 m, 10 October 1881, *Fish Hawk* stn 1047. North Carolina: 1 ♂, USNM, SE of Cape Lookout, 348-384 m, 13 November 1956, *Combat* stn 171. 1 ♂, USNM, SE of Cape Lookout, 329 m, 1 February 1972, *Oregon II* stn 11762. 1 ♂ 2 ♀, USNM, SE of Cape Fear, 187-190 m, 29 February 1960, *Silver Bay* stn 1693. Georgia: 1 ♀, USNM, off Ossabaw, 238 m, 21 January 1972, *Oregon II* stn 11720. Florida: 1 ♂, USNM, off Melbourne Beach, 329 m, 31 January 1957, *Combat* stn 226. 1 ♀, USNM, off Hobe Sound, 302-285 m, 21 May 1968, *Gerda* stn 997. 1 ♀, AMNH, 21 km E of Boynton, 320-266 m, 17 May 1948, Burey. 1 ♀, RMNH, off Miami, 418 m, 27/28 August 1962, *Gerda* stn 53. 1 ♀, RMNH, E of Old Rhodes Key, 146 m, 25 September 1964, *Gerda* stn 427. 2 ♀, USNM, off Elliott Key, 194-187 m, 25 August 1967, *Gerda* stn 857. 1 ♀, UMML, NE of Key Largo, 265-275 m, 24 January 1964, *Gerda* stn 229. 3 ♂ 3 ♀, USNM, SE of Key Largo, 185 m, 22 January 1965, *Gerda* stn 452. 1 ♀, RMNH, SW of Marquesas Keys, 188-199 m, 28 November 1964, *Gerda* stn 432. 1 ♂, USNM, SW of Marquesas Keys, 177-229 m, 26 April 1969, *Gerda* stn 1087. 1 ♂, UMML, S of Dry Tortugas Is, [?] 68 m, 12 April 1965, *Gerda* stn 564. 1 ♀, USNM, SW of Dry Tortugas, 348 m, 13 April 1954, *Oregon* stn 1005. 1 part of carapace,

USNM, NW of Charlotte Harbor, 274 m, 22 August 1970, *Oregon II* stn 11181.

BAHAMAS—2 ♀, RMNH, W of Gun Cay I, 458-531 m, 30 January 1964, *Gerda* stn 242. 1 ♀, RMNH, N of Double Headed Shot Cays, 443 m, 27 January 1965, *Gerda* stn 483.

LESSER ANTILLES—3 ♂ 1 ♀, USNM, E of The Grenadines, 357-658 m, 4 July 1969, *Pillsbury* stn 861.

WESTERN CARIBBEAN—1 ♀, USNM, W of Old Providence I, 549 m, 12 September 1957, *Oregon* stn 1918.

PANAMA—1 ♀, USNM, Golfo de los Mosquitos, 274-293 m, 31 May 1962, *Oregon* stn 3597.

VENEZUELA—1 ♀, USNM, E of Península de Paraguaná, 366 m, 4 October 1963, *Oregon* stn 4421. 1 ♂, USNM, off San Juan de los Cayos, 384 m, 9 October 1963, *Oregon* stn 4440.

TRINIDAD - TOBAGO—2 ♂, USNM, NW of Tobago, 146 m, 2 July 1969, *Pillsbury* stn 848.

BRAZIL—Alagoas: 1 ♂, BMNH, off Barra Grande, 10 September 1873, *Challenger* stn 122-122C.

Description.–Carapace (Figure 50) finely pubescent; setae dense and long on base of rostrum, gastric, and epigastric regions; small setae on cardiac region, and minute ones sparsely set on hepatic and branchial regions; abdomen polished, and almost entirely naked except for setae on posterodorsal keel; pubescence of telson as in Figure 46*B*. Rostrum short, its length 0.25-0.30 that of carapace, reaching little beyond midlength of first antennular article, almost horizontal, with dorsal margin straight and ventral margin strongly convex but with subapical concavity giving rise to saber shaped tip; latter 0.3-0.4 length of rostrum. Rostral plus epigastric teeth 6, apex of third rostral tooth or fourth tooth at level of orbital margin. Adrostral carina extending from orbital margin to ultimate tooth; postrostral carina ending immediately behind cervical sulcus. Orbital margin produced anteriorly in ventrally inclined short shelf. Postorbital spine, longest of four lateral spines on carapace, situated dorsal to base of small antennal spine; branchiostegal and hepatic spines sharp. Cervical sulcus deep, ending dorsally just posterior to midlength of carapace at base of postrostral carina; cervical carina sharp; hepatic sulcus almost horizontal posteriorly, inclined anteroventrally from depressed area below hepatic spine to pit below branchiostegal spine.

Eye as illustrated (Figure 44*B*).

Antennular peduncle length equivalent to about 0.65 that of carapace; prosartema long, conspicuously overreaching distomesial margin of first article; stylocerite length about 0.65 of distance between lateral base of first article and base of distolateral spine; latter slender and long; flagella long, length of dorsal flagellum 1.9 cl in shrimp 23 mm cl, proximal portion of flagellum slightly broader than subfiliform distal portion; ventral flagellum slightly shorter and broader than dorsal, gently tapering distally, and bearing long, marginal plumose setae. Scaphocerite overreaching antennular peduncle by as much as 0.2 of its own length, gently tapering from base to narrow distal portion; lateral rib ending in long, slender spine, barely or conspicuously overreaching distal margin of lamella. Antennal flagellum long, at least 3 times total length of shrimp. Mandibular palp with distal article slightly shorter than basal and almost reaching or barely overreaching distal margin of carpocerite. Third maxilliped surpassing antennular peduncle by length of dactyl and 0.2-0.5 length of propodus.

First pereopod stout, reaching between midlength and distal end of carpocerite. Second pereopod moderately stout, extending almost to distal end of carpocerite or overreaching it by not more

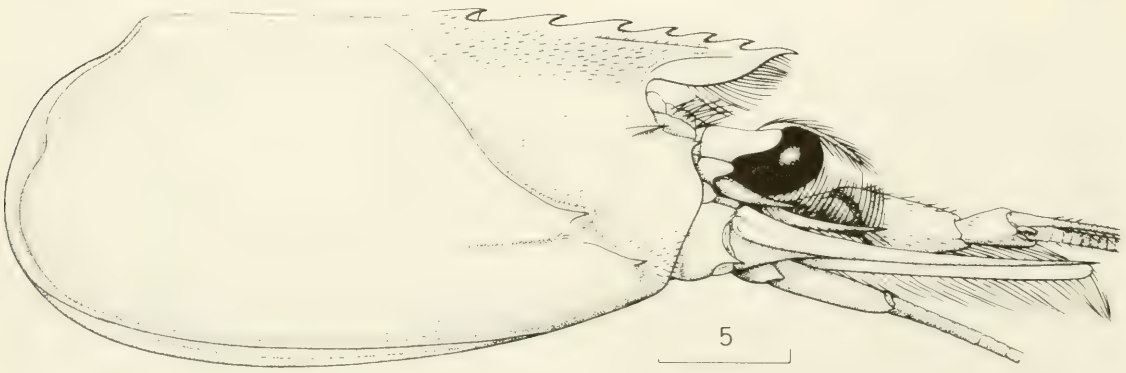

FIGURE 50.—*Hadropenaeus modestus*, 19 mm cl, west of Isla de Providencia, western Caribbean. Cephalothorax, lateral view.

than 0.5 length of dactyl. Third pereopod rather slender, exceeding antennular peduncle by tip or by entire length of dactyl. Fourth pereopod very slender, shorter than third, surpassing carpocerite by tip or by entire length of dactyl; length of dactyl 0.65-0.75 that of propodus; length of carpus about 1.1 times that of merus. Fifth pereopod very slender and long, overreaching antennular peduncle at least by length of dactyl and propodus, and at most by their length and 0.2 length of carpus. Order of pereopods in terms of their maximal anterior extensions; first, second, fourth, third, and fifth. First pereopod with very long, slender spine on basis, small spine on distomesial margin of ischium, and rather minute one near midlength of mesial margin of merus. Second pereopod with long spine on basis. Coxa of fourth and fifth pereopods in males armed with anterior spine. Coxa of fifth pereopod in females mesially produced into short plate, lacking spine on anteromesial margin; minute spine present in young.

Abdomen with high, sharp, median keel from fourth through sixth somites, low, rounded carina sometimes present on third; posterodorsal margin of third, fourth, and fifth somites with median incision; sixth somite bearing sharp spine at posterior end of keel, and minute spine on posteroventral angles. Telson (Figure 46*B*) with median sulcus deep anteriorly, disappearing well anterior to terminal portion; fixed lateral spines relatively short, their length 0.7-0.8 basal width of terminal portion; latter broad, length 2.5-3.3 times basal width; mesial ramus of uropod overreaching apex of telson by as much as 0.2 of its own length; lateral ramus conspicuously surpassing mesial, and armed with small distolateral spine, slightly projecting beyond contiguous distal margin of ramus.

Petasma (Figure 51*A*, *B*) cincinnulate along proximal 0.6 of median line; broad distal part of ventromedian lobule strongly produced into elongate, distally directed distomesial projection, and short distolateral projection, and with terminal margin spinulous; distal part of ventrolateral lobule heavily sclerotized, forming plate with border undulate adjacent to ventral costa, its terminal portion subrectangular, strongly inclined toward, and partially covered by, ventro-

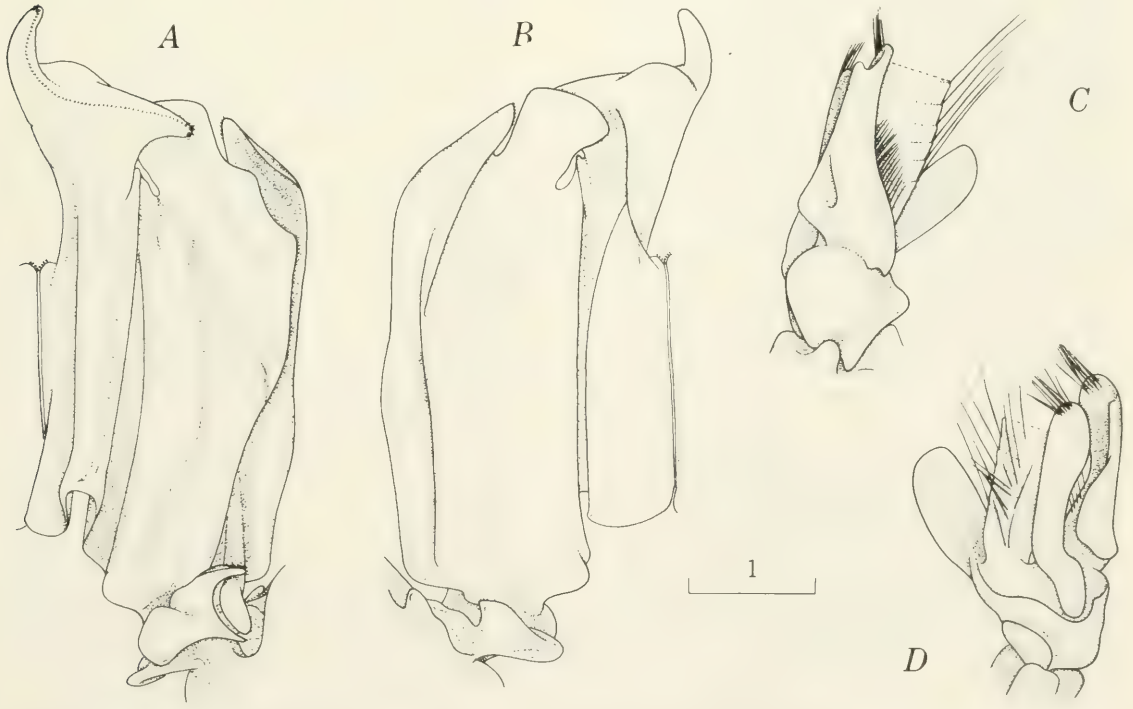

FIGURE 51.—*Hadropenaeus modestus*, ♂ 16.5 mm cl, southeast of Cape Fear, N.C. *A*, Petasma (partly bent laterally), dorsal view of right half. *B*, Ventral view. *C*, Right appendices masculina and interna, dorsal view. *D*, Ventromesial view.

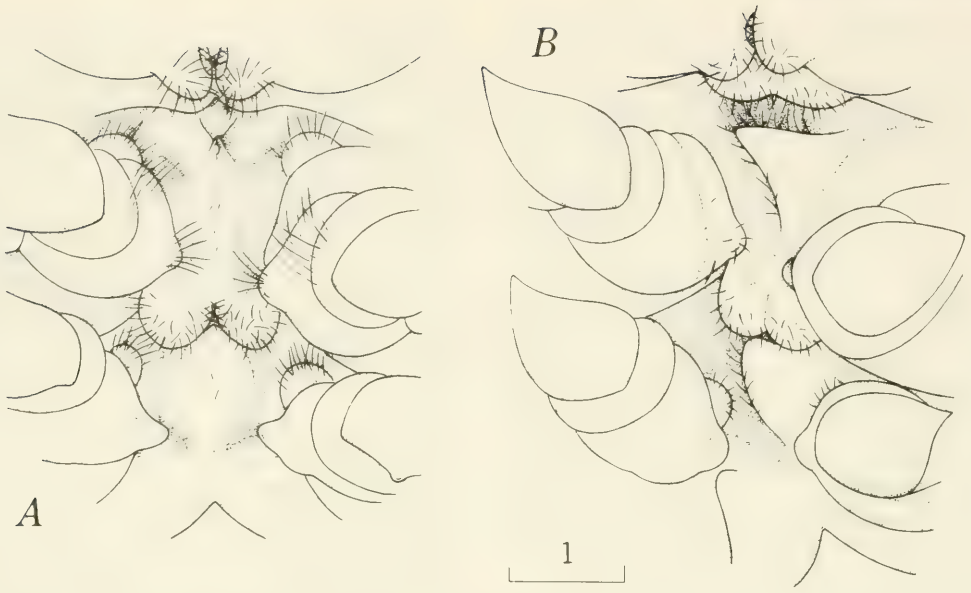

FIGURE 52.—*Hadropenaeus modestus*, holotype ♀ 8 mm cl, off Bethany Beach, Del. *A*, Thelycum, ventral view. *B*, Ventrolateral view.

median lobule; ventral costa with distal part free from contiguous plate, bent outward and bearing minute spinules on distalmost margin.

Appendix masculina and appendix interna together with ventrolateral spur (Figure 51*C, D*) similar to those of *H. affinis* (see above).

Thelycum (Figure 52*A, B*) with median protuberance on sternite XIV pyriform or subovate, its apical portion directed anteriorly, and lying between prominent, setose, paired convexities of posteriormost part of sternite XIII; longitudinal, high, median keel on sternite XIII produced anteriorly into ventrally or posteroventrally directed blunt tooth, with anterior margin straight or convex and posterior margin concave.

Maximum size.–Females: 19.5 mm cl; males: 17.5 mm cl.

Geographic and bathymetric ranges.–Off Delaware Bay (38°31′N, 73°21′W), to the Straits of Florida, and in the Gulf of Mexico, northwest of Charlotte Harbor, Fla.; also from the Bahamas, throughout the Caribbean to off Barra Grande (about 9°10′S, 34°52′W), Brazil (Figure 49). This species has been recorded at a depth range of about 150-550 m (Figure 9).

Affinities.–Hadropenaeus modestus may be readily distinguished from its close relative *H. affinis* by the characters included in Table 1.

Remarks.–I have examined the holotype of *H. modestus* and found that, contrary to the data presented by Smith (1885), it possesses 6 rostral teeth (including epigastric), not 7, and that the merus of the fourth pereopod is only 6.5 mm long, not 7.5 mm. Therefore the carpus, which is 7.2 mm long, is not shorter than the merus, but about 1.1 times the length of the latter. These incorrect statements led Bouvier (1906b) to point out differences in the rostral armature and relative length of the carpus between *H. modestus* and *H. affinis* which do not exist.

Hadropenaeus modestus is newly reported here in the Caribbean and the Atlantic off northeast South America. The locality record from off Barra Grande, Brazil, is based on a single male taken during the voyage of the *Challenger* (1873-76). On the label accompanying this specimen is "Barra Grande, Brazil, *Challenger*." Although there are several towns in Brazil bearing the name Barra Grande, the locality referred to above must be that in the State of Alagoas, because according to Tizard et al. (1885), the white cliffs of Barra Grande could be seen from *Chal-*

lenger stn 122, 122A, 122B, and 122C, which are between 9°5′ and 9°10′S. This specimen has not been recorded in the literature previously—probably because it is a juvenile, not readily identifiable.

Hadropenaeus lucasii (Bate 1881)

Figures 9, 16, 44C, 53-55

Solenocera lucasii Bate 1881:185 [holotype: ♀, BMNH, off Kai Is, south of New Guinea, 5°49′15″S, 132°14′15″E, 140 fm (256 m), 26 September 1874, *Challenger* stn 192]. [Not *Solenocera lucasii*. Miers 1884:15. Rathbun 1906:904, pl. 20, fig. 9.]

Philonicus lucasii. Bate 1888:277, pl. 42, fig. 4. ? Thomson 1904:254.

Pleoticus lucasii. Bate 1888:939.

Haliporus modestus. Rathbun 1906:905, pl. 20, fig. 4. [Not *Hymenopenaeus* [*Hadropenaeus*] *modestus* Smith 1885.]

Haliporus lucasi. Bouvier 1908:80.

?*Haliporus malhaensis* Borradaile 1910:258, fig. 2 [type not extant; type-locality: off Saya de Malha, Indian Ocean, 145 fm (265 m)]. de Man 1911:7.

Haliporus lucasii. de Man 1911:7.

Hymenopenaeus lucasii. Burkenroad 1936:104. Anderson and Lindner 1945:289. Kubo 1949: 213, fig. 8 B[1], 20 Q, 27 K-N, 66 O, P, 72 C, I, 80 H, 91, 92 A, C.

?*Hymenopenaeus lucassi*. Ramadan 1938:57.

Hymenopenaeus lucasi. Crosnier and Forest 1973: 256, fig. 83a.

Material

HAWAII—6 ♂ 5 ♀, USNM, Pailolo Channel, 271-223 m, 23 July 1902, *Albatross* stn 4101. 1 ♂ 1 ♀, USNM, Pailolo Channel, 223-241 m, 23 July 1902, *Albatross* stn 4102. 1 ♀, USNM, Pailolo Channel, 241-258 m, 23 July 1902, *Albatross* stn 4103. 1 ♀, USNM, N coast of Maui I, 369-402 m, 21 July 1902, *Albatross* stn 4081. 3 ♂ 10 ♀, USNM, NW coast of Maui I, 214 m, 16 November 1968, *Townsend Cromwell* stn 40-43. 4 ♀, USNM, NW coast of Maui I, 218 m, 17 November 1968, *Townsend Cromwell* stn 40-48. 4 ♂ 12 ♀, USNM, NW coast of Maui I, 218 m, 17 November 1968, *Townsend Cromwell* stn 40-49. 1 ♂ 12 ♀, USNM, NW coast of Maui I, 216-232 m, 28 April 1968, *Townsend Cromwell* stn 36-11. 1 ♂ 16 ♀, USNM, Kaiwi Channel, 177-183 m, 5 May 1968, *Townsend Cromwell* stn 36-26. 3 ♀, USNM, S coast of Oahu I, 538-470 m, 6 May 1902, *Albatross* stn 3920. 2 ♀, USNM, N coast of Oahu I, 176-201 m, 12 July 1972, *Townsend Cromwell* stn 59-3. 2 ♂, USNM, NW coast of Oahu I, 395-459 m, 25 July 1902, *Albatross* stn 4121. 1 ♂ 1 ♀, USNM, vicinity of Laysan I, 271-298 m, 16 May 1902, *Albatross* stn 3938. 1 ♂, USNM, vicinity of Laysan I, 364-177 m, 19 May 1902, *Albatross* stn 3947.

NEW GUINEA—1 ♀ holotype, BMNH, off Kai Is, 256 m, 26 September 1874, *Challenger* stn 192.

REPUBLIC OF MALDIVES—1 ♀, BMNH, off Maldive Is, 256-293 m, 4 April 1934, The John Murray Expedition stn 153.

MADAGASCAR—1 ♂, USNM, NW of Baie du Currier, 350-360 m, 15 September 1972, A. Crosnier.

Description.–Carapace (Figure 53) with restricted pubescent areas: setae dense and long at base of rostrum, on pterygostomian region, and in patch extending from orbital margin to epigastric tooth. Abdomen polished and naked; telson with rows of minute setae flanking median sulcus and lateral margins; mesial ramus of uropod sparsely pubescent. Rostrum short, its length 0.30-0.35 that of carapace, reaching to, or almost to, distal margin of first antennular article, horizontal, with dorsal margin straight and ventral margin strongly

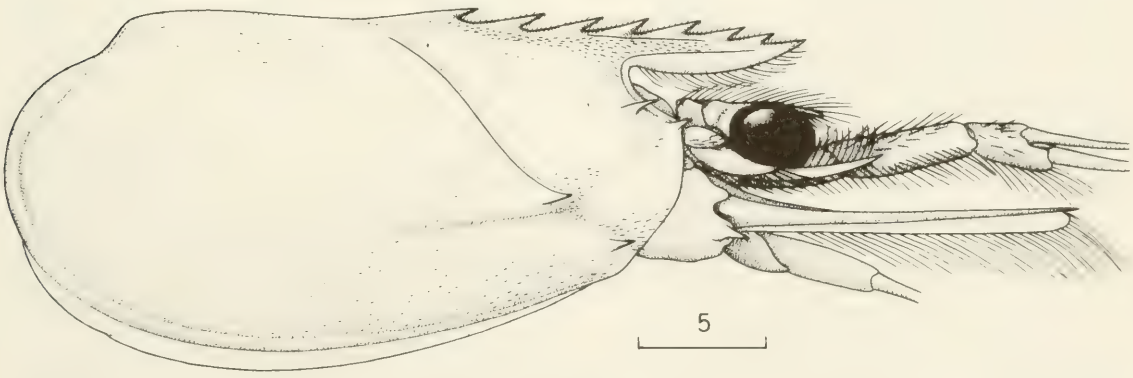

FIGURE 53.—*Hadropenaeus lucasii*, ♀ 18.5 mm cl, northwest coast of Maui, Hawaiian Islands. Cephalothorax, lateral view.

convex; tip about 0.2 length of rostrum. Rostral plus epigastric teeth 6-8 (mode 7; percentage distribution: 6-13.3, 7-83.3, 8-3.3; $N = 60$); third rostral tooth usually situated at level of orbital margin. Adrostral carina extending from orbital margin to base of ultimate tooth, and shorter, more dorsal, conspicuous carina extending from second rostral tooth to penultimate; postrostral carina ending immediately behind cervical sulcus. Orbital margin produced anteriorly into ventrally inclined, short shelf. Postorbital spine, longest of four lateral spines on carapace, usually more slender than middorsal teeth on carapace, and located dorsal to base of small antennal spine; branchiostegal and hepatic spines sharp. Cervical sulcus deep, ending dorsally just anterior to midlength of carapace, near postrostral carina; cervical carina sharp; hepatic sulcus subhorizontal posteriorly, originating almost at level of dorsal extremity of cervical sulcus, shallow and inclined anteroventrally from depressed area below hepatic spine to pit below branchiostegal spine.

Eye as illustrated (Figure 44*C*).

Antennular peduncle length equivalent to 0.65 that of carapace; prosartema long, conspicuously overreaching distomesial margin of first article; stylocerite length about 0.65 of distance between its proximal extremity and mesial base of distolateral spine; latter very slender and long, considerably surpassing proximal margin of second article. Antennular flagella long and considerably unequal in length, dorsal 1.85 times carapace length and ventral 1.30 in shrimp 12.5 mm cl, and 1.35 and 0.90, respectively, in shrimp 27 mm cl; dorsal flagellum subcylindrical, ventral subcylindrical to depressed. Scaphocerite reaching to distal margin of antennular peduncle or overreaching it by as much as 0.15 of its own length; lateral rib ending in spine reaching to, or slightly beyond, distal margin of lamella. Antennal flagellum long, although incomplete in all specimens, longest observed 3 times total length of shrimp. Mandibular palp with article as long as or slightly shorter than basal, reaching between midlength and distal 0.35 of carpocerite. Third maxilliped reaching to midlength of third antennular article or overreaching it by as much as 0.5 length of propodus; length of dactyl 0.75 that of propodus.

First pereopod, stoutest of five, reaching between midlength and distal 0.15 of carpocerite. Second pereopod extending to distal end of carpocerite or overreaching it by as much as entire length of dactyl. Third pereopod overreaching antennular peduncle by 0.5 length of dactyl or by

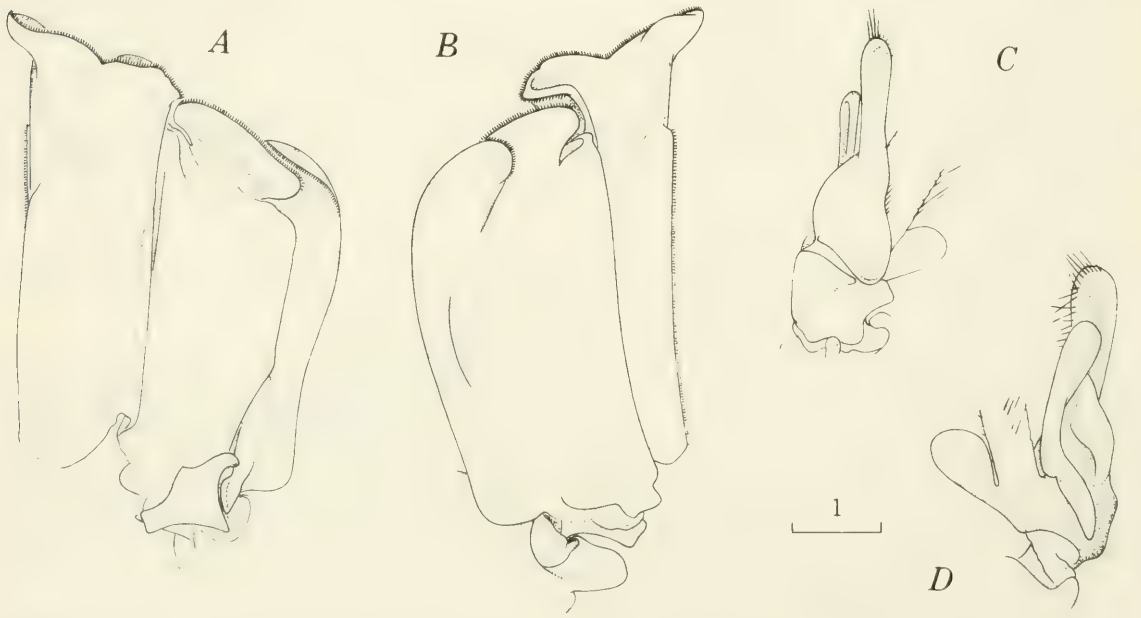

FIGURE 54.—*Hadropenaeus lucasii*, ♂ 13 mm cl, Pailolo Channel, Hawaiian Islands. *A*, Petasma (partly bent laterally), dorsal view of right half. *B*, Ventral view. *C*, Right appendices masculina and interna, dorsolateral view. *D*, Ventromesial view.

as much as entire propodus. Fourth pereopod exceeding carpocerite by almost length of dactyl and sometimes by as much as length of dactyl and 0.15 that of propodus. Fifth pereopod reaching beyond antennular peduncle by length of dactyl and 0.6 to entire length of propodus. Order of pereopods in terms of their maximal anterior extensions: first, second, fourth, third, and fifth. First pereopod bearing very long spine on distomesial extremity of basis, long one on that of ischium, and relatively small spine almost at midlength of merus. Second pereopod with long spine on basis. In female, coxa of third pereopod produced mesially into rather short densely setose plate; coxa of fourth pereopod bearing narrow plate. In both sexes, coxa of fourth and fifth pereopods bearing conspicuous anterior spine.

Abdomen with strong middorsal carina from third through sixth somites, carina rounded on third, forming keel from fourth posteriorly; posterodorsal margin of third, fourth, and fifth with long median incision; sixth somite length about 1.3 times maximum height, bearing sharp spine at posterior end of keel and minute spines at posteroventral angles. Telson with median sulcus deep anteriorly, progressively shallower posteriorly, disappearing just before reaching base of lateral spines; terminal portion length 3.3-4.0 times basal width; lateral spines short, 1-1.4 times basal width of terminal portion. Mesial ramus of uropod reaching to, or slightly surpassing, apex of telson; lateral ramus overreaching mesial by as much as 0.2 of its own length, and armed with minute distolateral spine, reaching distal margin of ramus.

Petasma (Figure 54*A, B*) cincinnulate along proximal 0.70 of median line; broad distal part of ventromedian lobule produced into blunt, distomesial projection, its lateral part turned strongly inward; entire terminal margin of lobule spinulous; distal part of ventrolateral lobule heavily sclerotized, forming plate, border adjacent to ventral costa bearing emargination delimiting basal part from short, broadly subelliptical terminal part; latter inclined toward, and partially covered by, ventromedian lobule, and armed with spinules along entire distal margin; ventral costa with distal part free from, and falling short of, contiguous plate, its distal margin bearing very minute spinules.

Appendix masculina (Figure 54*C, D*) with proximal part broad, produced mesially into thickened lobe, and bearing long setae along lateral margin; distal part narrow, directed strongly laterally, and bearing apical tuft of long setae. Appendix interna shorter than appendix masculina, narrow, and lacking setae. Ventrolateral spur large, paddlelike.

Thelycum (Figure 55) with median protuberance on sternite XIV roughly elliptical, low, markedly less elevated than prominent setose, paired convexities of sternite XIII; median ridge of latter long, lacking tooth, sometimes ending in small knob at one or both extremities.

Maximum size.–Female (holotype), 25.5 mm cl, 100 mm tl; male, 18.5 mm cl, 72.5 mm tl (Kubo 1949). Largest male examined by me, 14 mm cl, about 64 mm tl.

Geographic and bathymetric ranges.–Madagascar (off northwest coast) through the Indo-West Pacific to Hawaii (Figure 16), in depths between 180 and 500 m (Figure 9). The few records available are from scattered localities.

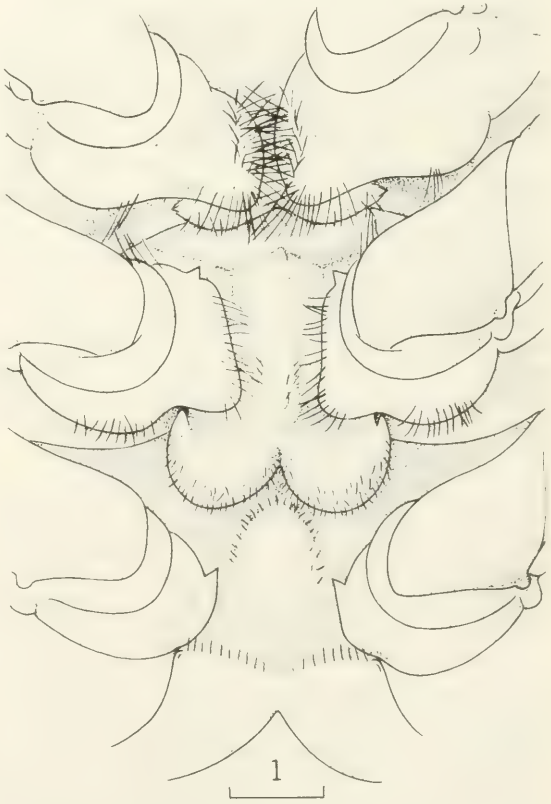

FIGURE 55.—*Hadropenaeus lucasii,* ♀ 19.5 mm cl, Pailolo Channel, Hawaiian Islands. Thelycum, ventral view.

Affinities.–Hadropenaeus lucasii is closely allied to its two Atlantic congeners, *H. affinis* and *H. modestus,* but it may be distinguished from them by the possession of a conspicuous carina on the rostrum dorsal to the adrostral carina, and by certain petasmal and thelycal features. In *H. lucasii* the ventromedian lobule of the petasma is not produced into a distolateral projection; instead, its lateral portion is turned strongly inward; the distal plate of the ventrolateral lobule bears spinules along the entire terminal margin and is produced in a blunt, ventral projection; in addition, the ventral costa falls conspicuously short of the distalmost part of the adjacent plate. The thelycum, in turn, is characterized by a median protuberance on sternite XIV, which does not project ventrally so far as the posterior convexities of sternite XIII, and the latter bears a low median ridge which is not produced anteriorly in a large tooth. Furthermore, in females of *H. lucasii,* the coxae of the fourth pair of pereopods bear a conspicuous anteromesial spine which is lacking in the other two species.

Hadropenaeus lucasii exhibits some morphological variations which are undoubtedly taxonomically insignificant because extremes of variations occur in animals from the same region and even from the same locality. Among them are the relative extension of the scaphocerite, gnathal and thoracic appendages, the total number of rostral teeth as well as the number situated on the carapace. The evidence at hand, however, indicates that the ventral antennular flagellum and some features of the petasma differ regionally. The ventral antennular flagellum is somewhat depressed in the holotype from New Guinea, in Japanese specimens (Kubo 1949) and in two specimens from Madagascar examined by me, and subcylindrical in individuals from Indonesia (de Man 1911) as well as in all those available from Hawaii. In addition, the distomesial projections of the ventromedian lobules of the petasma are larger in specimens from Japan than in males from Madagascar and Hawaii. Whereas the shape of the flagellum exhibits definite variations which seem to be regionally restricted, the differences in the petasma are limited to degree of development and are perhaps insignificant. Except for the collection from Hawaii, available material is extremely meager; consequently, the variations that I have noted are pointed out, with the conviction that definite conclusions as to their taxonomic value must await examination of adequate collections from various areas throughout the Indo-West Pacific.

I have examined the female from the Maldive Islands, Indian Ocean, that Ramadan (1938) identified as *H. lucasii.* This specimen differs from other specimens of the latter species in the following features: the rostral and epigastric teeth are slenderer—not much stronger than the postorbital spine—and inclined more anteriorly; the anteromesial spine on the coxa of the fifth pereopod is longer and more slender; and the median protuberance on sternite XIV is smaller and surrounded by a shallow depression. Crosnier and Forest (1973), who presented an illustration of the thelycum of the specimen (plate 85, figure a), suggested that the slight differences between the thelycum of the latter and that of the type of *H. lucasii* could be due to the difference in size of the animals, the type being 90 mm long (23.5 mm cl) and Ramadan's specimen 70 mm. As these authors indicated, Ramadan's specimen exhibits 6 middorsal teeth (rostral plus epigastric), 3 of which are located on the carapace; this number and arrangement of teeth occurs infrequently in members of *H. lucasii,* but has been observed in several specimens by both Rathbun (1906) and me. Crosnier and Forest suggested further that because of the number and arrangement of the middorsal teeth and the relative size of those behind the rostrum (which are not much stronger than the postorbital spine), Ramadan's specimen might be referable to Borradaile's (1910) *Haliporus malhaensis.* This species was described from Saya de Malha, Indian Ocean, and its identity is still uncertain, primarily because the holotype, the only specimen on which the description was based, is no longer extant (Ramadan 1938). The features pointed out above suggest that the shrimp from the Maldive Islands might belong to a species other than *H. lucasii,* but an understanding of its systematic position must await more material from the Indian Ocean.

Both Burkenroad (1936) and Ramadan (1938) were inclined to think that *H. malhaensis* was identical with *H. lucasii,* and placed the former name in the synonymy of the latter preceded by a question mark. Previously, de Man (1911) had indicated that he would have identified them as one species, except for Borradaile's statement that in *H. malhaensis* neither the fourth nor the fifth pereopod is "particularly slender." De Man also called attention to the fact that in Borradaile's illustration the propodi of the fourth and fifth

pereopods are missing. Kubo (1949) considered that *H. malhaensis* and *H. lucasii* are distinct species; he stated that his specimens of *H. lucasii* cannot be referred to *H. malhaensis* because in the latter there are 3 teeth on the carapace, the scaphocerite does not overreach the antennular peduncle, and the dorsal antennular flagellum is not longer than the ventral which also lacks "rather long setae" on the dorsal and ventral borders. Actually, the first two features are not typical of *H. malhaensis* but occur in *H. lucasii,* in which, as stated above, 3 teeth may be present on the carapace, and the scaphocerite, which usually overreaches the antennular peduncle, extends only to the distal end of the peduncle in some individuals. Features of the antennular flagella of *H. malhaensis* cited by Kubo could be due to the fact that the dorsal flagellum was incomplete in the type, as it often is in preserved specimens, or to omissions of the artist. The two species discussed seem to me to be quite similar, and if there is doubt in my mind as to the status of *H. malhaensis,* it is mainly because of Borradaile's statement that the fourth and fifth pereopods are not "particularly slender." The species exhibits most of the features of *Hadropenaeus:* stout body, thick carapace, short rostrum with ventral margin convex, middorsal teeth on the carapace separated by regularly decreasing intervals, lack of branchiocardiac carina and sulcus, and relative length of the last two pereopods having "fourth leg rather longer and fifth considerably longer than the third." These features of *Hadropenaeus* combined with a fifth pereopod that is not very slender, however, are unique. Perhaps the question of the identity of Borradaile's species will be resolved when large collections of solenocerids from the Indian Ocean are studied. Meanwhile, I am inclined, tentatively, to assign *H. malhaensis* to the synonymy of *H. lucasii.*

Mesopenaeus New Genus

Parartemesia Bouvier 1905b:747 [part, excluding *Parartemesia carinata* Bouvier 1905b = *Pleoticus muelleri* (Bate 1888)].
Haliporus. Bouvier 1906b:1 [part]; 1908:78[part]. A. Milne Edwards and Bouvier 1909:206 [part].
Hymenopenaeus. Burkenroad 1936:102 [part]. Roberts and Pequegnat 1970:29 [part].

Diagnosis.–Body stout, carapace proportionately short; integument thick, firm. Rostrum short, reaching approximately to base of second antennular article; deep, with ventral margin pronouncedly convex, and armed only with dorsal teeth; epigastric tooth and first rostral separated by interval similar to that between first and second rostral teeth. Orbital, postorbital, antennal, and hepatic spines present; pterygostomian and branchiostegal spines absent. Cervical sulcus long, almost reaching middorsum of carapace; hepatic sulcus deep; branchiocardiac carina and sulcus, posthepatic, and submarginal carinae lacking. Abdomen carinate dorsally from third through sixth somites. Telson with pair of conspicuous, fixed lateral spines. Prosartema long, flexible. Antennular flagella not much longer than carapace and dissimilar: dorsal flagellum subcylindrical and slender, ventral one conspicuously depressed. Mandibular palp two jointed, articles broad, distal one almost as long as basal and tapering to blunt apex. First maxilla with unsegmented palp (endite of basis) gently narrowing to rounded apex. Fourth and fifth pereopods rather stout proximally, fifth moderately longer than fourth. First pereopod with spine on basis and ischium. Exopods on all maxillipeds and pereopods. Lateral ramus of uropod armed with distolateral spine reaching distal margin of lamella (terminal). In males, petasma with ventral costa not projecting free distally, there bearing flexible flap; distal portion of rib of dorsolateral lobule projecting beyond margin of adjacent area; endopod of second pleopod bearing appendices masculina and interna, and with basal sclerite produced distally into long ventrolateral spur. Thelycum of open type, lacking enclosed seminal receptacle. Pleurobranchia on somites IX to XIV; single, rudimentary arthrobranchia on VII, and anterior and posterior arthrobranchiae on somites VIII to XIII; podobranchia on second maxilliped, and epipod on second maxilliped (and on first if proximal exite of coxa considered an epipod) through fourth pereopod.

Type-species.–Parartemesia tropicalis Bouvier 1905b.

Etymology.–The generic name is derived from the Greek mesos, something in between, in combination with the generic name *Penaeus,* alluding to the fact that the dorsal antennular flagellum is subcylindrical and filiform, as in *Pleoticus, Haliporoides* and *Hymenopenaeus,* and the ventral one flattened, much as in *Solenocera.*

Gender.–Masculine.

List of species.–This genus includes only one species: the western Atlantic *Mesopenaeus tropicalis* (Bouvier 1905b).

Affinities.–*Mesopenaeus* resembles *Solenocera* in possessing a flattened ventral flagellum, but in the former this appendage is neither so flattened and broad nor is it channeled as it is in the latter. It shares with its more closely allied genera—*Hymenopenaeus, Haliporoides, Pleoticus,* and *Hadropenaeus*—a subcylindrical dorsal flagellum, and a similar armature of the lateral ramus of the uropod, the lateral rib of which ends in a well-defined spine. The stout body, deep rostrum with the ventral margin pronouncedly convex, arrangement of the epigastric and rostral teeth, and absence of both branchiocardiac sulcus and carina place *Mesopenaeus* closer to *Hadropenaeus* than to the other genera. *Mesopenaeus* differs from *Hadropenaeus,* however, in that the ventral flagellum is invariably depressed, whereas in the latter it is almost always subcylindrical (in occasional individuals of *H. lucasii* the ventral flagellum is depressed). In *Mesopenaeus* orbital and branchiostegal spines are present, and the thelycum exhibits paired anterior protuberances on sternite XIV which are present elsewhere among the solenocerids only in the members of the nominal genus. Finally, in *Mesopenaeus* the ventral costa of the petasma is fused to the flexible terminal part of the ventrolateral lobule, whereas in *Hadropenaeus* the ventral costa is distally free from the sclerotized terminal part of the lobule.

Mesopenaeus tropicalis (Bouvier 1905)

Figures 9, 34, 56-63

Parartemesia tropicalis Bouvier 1905b:748 "mer des Antilles" in 80-175 fm (146-329 m). [No type designated.]

Haliporus tropicalis. Bouvier 1906b:4; 1908:80. A. Milne Edwards and Bouvier 1909:217, fig. 45-54, pl. 3, fig. 1-19 [lectotype ♀, MCZ 7199; type-locality: "Blake: Florida Bank, lat. N. 26° 31′, long. 0. 85° 03′, 119 brasses." Paralectotype ♀, MP, off Barbados, 13°04′12″N, 59°36′45″W, 76 fm (139 m), 5 March 1879, *Blake* stn 272]. de Man 1911:7.

Hymenopenaeus tropicalis. Burkenroad 1936:103. Springer and Bullis 1956:8. Boschi 1964:38. Bullis and Thompson 1965:5. Williams 1965:15, fig. 5-7. Cerame-Vivas and Gray 1966:263. Mistakidis and Neiva 1966:434. Roberts and Pequegnat 1970:29. Pequegnat and Roberts 1971:8. Iwai 1973:44, fig. 13.

Solenocera weymouthi Lindner and Anderson 1941:181, fig. 1a-e [holotype ♀, USNM 79357; type-locality: off Orange Beach, Ala., 29°28′N, 87°30′W, 46 fm (84 m), *Pelican* stn 137-2, 1 March 1939; allotype ♂, USNM 79359, 23 km S of Dry Tortugas, 110 m, 5 August 1932, *Anton Dohrn* stn 74-32; paratype ♂, USNM 79358, locality as in holotype; 71 ♂ 78 ♀, USNM 23420, between Cape Hatteras and Cape Lookout, N.C., 34°35′30″N, 75°45′30″W, 32 fm (59 m), 18 October 1885, *Albatross* stn 2605]. Anderson and Lindner 1945:286.

Hypenepenaeus tropicalis. Mistakidis 1965:9.

Material

UNITED STATES—North Carolina: 2 ♂ 1 ♀, UNC-IMS, NE of Cape Lookout, 90-110 m, 27 April 1965, *Eastward* stn 1087. 71 ♂ 78 ♀ (paratypes *Solenocera weymouthi*), USNM 23420, NE of Cape Lookout, 59 m, 18 October 1885, *Albatross* stn 2605. 1 ♀, USNM, SE of Cape Lookout, 82 m, 21 June 1957, *Combat* stn 406. 1 ♂ 1 ♀, UNC-IMS, SE of Cape Lookout, 229 m, 8 June 1949, *Albatross III* stn 21-4. 8 ♂ 8 ♀, USNM, SE of Cape Lookout, 154 m, 8 June 1949, *Albatross III.* 2 ♂ 4 ♀, UNC-IMS, E of Cape Fear, 100 m, 27 April 1965, *Eastward* stn 1089. 1 ♂, UNC-IMS, SE of Cape Fear, 140-145 m, 27 April 1965, *Eastward* stn 1086. 2 ♂ 2 ♀, USNM, SE of Cape Fear, 183 m, 29 January 1972, *Oregon II* stn 11747. 3 ♂ 5 ♀, USNM, off Cape Fear, 190-187 m, 29 February 1960, *Silver Bay* stn 1694. 1 ♂ 8 ♀, USNM, SE of Cape Fear, 187-190 m, 29 February 1960, *Silver Bay* stn 1693. South Carolina: 1 ♀, USNM, off Cape I, 183 m, 28 January 1972, *Oregon II* stn 11743. 1 ♀, USNM, E of Bull Bay, 181 m, 5 January 1885, *Albatross* stn 2313. 2 ♀, USNM, E of Bull Bay, 155 m, 5 December 1960, *Silver Bay* stn 2535. 1 ♀, USNM, off Santa Helena Sound, 83 m, 28 April 1966, *Oregon* stn 6073. Georgia: 4 ♀, USNM, off Savannah, 68-91 m, 14 December 1961, *Silver Bay* stn 3658. 7 ♂ 2 ♀, USNM, off Savannah, 73 m, 12 March 1956, *Bowers* stn 54. 1 ♀, USNM, off Savannah Beach, 73 m, 26 April 1966, *Oregon* stn 6062. 1 ♂, USNM, off Catherines Sound, 37 m, 13 March 1940, *Pelican* stn 195-10. Florida: 1 ♀, USNM, off Fernandina, 179 m, 18 January 1972, *Oregon II* stn 11699. 1 ♂ 9 ♀, USNM, off St Augustine, 75 m, 24 April 1966, *Oregon* stn 6044. 1 ♂ 3 ♀, USNM, off St Augustine, 40 m, 5 September 1962, *Silver Bay* stn 4340. 1 ♀, USNM, off Matanzas Inlet, 183 m, 18 November 1965, *Oregon* stn 5741. 1 ♀, USNM, off Matanzas Inlet, 64-87 m, 7 October 1962, *Silver Bay* stn 4451. 1 ♀, USNM, off Ponce de Leon Inlet, 73-97 m, 5 October 1962, *Silver Bay* stn 4420. 1 ♂ 1 ♀, USNM, off Edgewater, 51-37 m, 24 August 1965, *Oregon* stn 5603. 1 ♀, USNM, off Cape Kennedy, 70 m, 16 January 1966, *Oregon* stn 5860. 1 ♀, USNM, off Melbourne Beach, 73 m, 14 July 1961, *Silver Bay* stn 3279. 1 ♀, UMML, NE of St Lucie Inlet, 38-42 m, 21 May 1968, *Gerda* stn 1002. 1 ♂, UMML, SE of St Lucie Inlet, 60-62 m, 21 May 1968, *Gerda* stn 1001. 1 ♀, RMNH, E of Miami, 119 m,

16 April 1965, *Gerda* stn 622. 3 ♀, RMNH, off Elliott Key, 82-77 m, 15 April 1965, *Gerda* stn 610. 2 ♀, USNM, off Old Rhodes Key, 91 m, 10 November 1961, *Silver Bay* stn 3524. 2 ♂ 3 ♀, USNM, off Key Largo, 86-79 m, 10 July 1967, *Gerda* stn 834. 1 ♂ 2 ♀, RMNH, off Key Largo, 86-95 m, 14 September 1965, *Gerda* stn 752. 1 ♂ 2 ♀, RMNH, off Key Largo, 92-97 m, 14 September 1965, *Gerda* stn 751. 1 ♀, UMML, off Key Largo, 108-88 m, 26 January 1966, *Gerda* stn 767. 2 ♀, RMNH, off Key Largo, 146 m, 26 January 1966, *Gerda* stn 770 . 1 ♀, USNM + 4 ♂ 2 ♀, RMNH, off Key Largo, 99-91 m, 10 July 1967, *Gerda* stn 833. 4 ♂ 2 ♀, RMNH, SE of Key Largo, 95 m, 15 April 1965, *Gerda* stn 602. 1 ♂ 1 ♀, USNM, off Key Largo, 102 m, 9 April 1886, *Albatross* stn 2639. 1 ♀, USNM, Hawk Channel, 110 m, 27 October 1960, *Silver Bay* stn 2391. 1 ♂ 9 ♀, USNM, Hawk Channel, 128 m, 27 October 1960, *Silver Bay* stn 2392. 1 ♂ 1 ♀, USNM, SE of Key West, 93-106 m, 25 February 1969, *Gerda* stn 1024. 2 ♂ 2 ♀, USNM, SE of Key West, 135-146 m, 25 February 1969, *Gerda* stn 1028. 2 ♂, USNM, off Key West, 179 m, 14 February 1902, *Fish Hawk* stn 7279. 1 ♂, USNM, SW of Marquesas Keys, 196-210 m, 26 April 1969, *Gerda* stn 1084. 1 ♂, USNM, SW of Marquesas Keys, 201-210 m, 26 April 1969, *Gerda* stn 1085. 2 ♀, USNM, SW of Marquesas Keys, (depth not given), 12 December 1962, *Oregon* stn 4142. 2 ♂ 2 ♀, USNM, S of Dry Tortugas, 366 m, 10 July 1965, *Oregon* stn 1330. 1 ♂, USNM, S of Dry Tortugas, 229-274 m, 28 April 1969, *Gerda* stn 1095. ♂ (allotype *S. weymouthi*), USNM 79359, 23 km S of Dry Tortugas, 110 m, 5 August 1932, *Anton Dohrn* stn 74-32. 1 ♂, USNM, SW of Dry Tortugas, 348 m, 13 April 1954, *Oregon* stn 1005. 1 ♀, USNM, SW of Dry Tortugas, 183 m, 6 August 1963, *Oregon* stn 4370. 1 ♂ 21 ♀, USNM, NW of Dry Tortugas, 298 m, 19 April 1954, *Oregon* stn 1026. ♀ lectotype, MCZ 7199, Florida Bank, 218 m, *Blake*. 4 ♂ 1 ♀, USNM, off St Petersburg, 106 m, 18 March 1954, *Oregon* stn 938. 2 ♀, USNM, W of Clearwater, 146 m, 11 March 1956, *Oregon* stn 920. 6 ♂ 12 ♀, USNM, off Apalachicola Bay, 88 m, 10 March 1954, *Oregon* stn 917. 2 ♂ 7 ♀, USNM, S of St Vincent I, 64 m, 7 March 1954, *Oregon* stn 896. 1 ♂, USNM, off Panama City, 101-130 m, 26 July 1957, *Silver Bay* stn 100. 4 ♂ 3 ♀, USNM, off Choctawhatchee Bay, 91 m, 21 March 1954, *Oregon* stn 944. 2 ♀, USNM, off Gulf Beach, 165 m, 1 March 1955, *Oregon* stn 1254. Alabama: ♀ (holotype *S. weymouthi*), USNM 79357, off Orange Beach, 84 m, 1 March 1939, *Pelican* stn 137-2. 1 ♂ (paratype *S. weymouthi*), USNM 79358, same locality as holotype.

MEXICO—Quintana Roo: 2 ♂ 18 ♀, USNM, NE of Cape Catoche, 183 m, 22 January 1967, *Oregon* stn 6399.

BAHAMA ISLANDS—1 ♂ 3 ♀, USNM, NE of Little Bahama Bank, 183 m, 25 October 1961, *Silver Bay* stn 3466. 1 ♀, RMNH, Northwest Providence Channel, 278-329 m, 3 March 1965, *Gerda* stn 526. 1 ♂ 4 ♀, RMNH, off Great Isaac I, 311-329 m, 2 March 1965, *Gerda* stn 509. 1 ♂, USNM, off Dog Rocks, Cay Sal Bank, 618 m, 22 June 1967, *Gerda* stn 815. 1 ♀, USNM, off Great Inagua, 183-137 m, 5 November 1961, *Silver Bay* stn 3502. 1 ♂ 1 ♀, USNM, S of Great Inagua, 311 m, 13 December 1969, *Oregon II* stn 10849. 1 ♂ 4 ♀, USNM, S of Great Inagua, 311 m, 13 December 1969, *Oregon II* stn 10850.

CUBA—2 ♂, USNM, N of Las Villas, 461 m, 15 December 1969, *Oregon II* stn 10860.

DOMINICAN REPUBLIC—1 ♂ 1 ♀, USNM, off Cabo Engaño, 201 m, 17 October 1963, *Silver Bay* stn 5188.

PUERTO RICO—2 ♂ 2 ♀, USNM, Mona Passage, 366 m, 17 October 1963, *Silver Bay* stn 5190.

LESSER ANTILLES—2 ♀, USNM, Dominica Passage, 640 m, 1 December 1969, *Oregon II* stn 10825. 1 ♀, USNM, off Barbados, 91-366 m, J. B. Lewis. 1 ♀ paralectotype, MP, off Barbados, 139 m, 5 March 1878, *Blake* stn 272.

WESTERN CARIBBEAN—18 ♂ 12 ♀, USNM, Arrowsmith Bank, 311-146 m, 28 January 1968, *Gerda* stn 954. 1 ♂ 5 ♀, USNM, Arrowsmith Bank, 252-293 m, 14 March 1968, *Pillsbury* stn 591. 1 ♂ 2 ♀, USNM, Arrowsmith Bank, (depth not given), 15 November 1968, *Pillsbury* stn 598. 1 ♂, UMML, Arrowsmith Bank, 115-190 m, 23 August 1970, *Gerda* stn 1286. 1 ♂ 1 ♀, USNM, Arrowsmith Bank, 307-192 m, 28 January 1968, *Gerda* stn 951. 1 ♂, USNM, Arrowsmith Bank, 225-437 m, 21 August 1970, *Gerda* stn 1275. 1 ♀, USNM, NE of Banco Gorda, 265-274 m, 6 June 1962, *Oregon* stn 3622. 2 ♀, UMML, NW of Quita Sueño Bank, 296-375 m, 31 January 1971, *Pillsbury* stn 1356. 1 ♂ 1 ♀, USNM, W of Quita Sueño Bank, 201-207 m, 12 February 1967, *Oregon* stn 6460. 22 ♂ 24 ♀, USNM, W of Isla de Providencia, 289-274 m, 4 February 1967, *Oregon* stn 6423. 1 ♂ 5 ♀, USNM, SW of Isla de San Andrés, 201-219 m, 4 February 1967, *Oregon* stn 6424. 18 ♂ 20 ♀, USNM, W of Isla de San Andrés, 139 m, 6 February 1967, *Oregon* stn 6434. 6 ♂ 10 ♀, USNM, W of Cayos de Albuquerque, 192 m, 7 February 1967, *Oregon* stn 6444.

BELIZE—1 ♂ 3 ♀, USNM, W of Lighthouse Reef, 329-274 m, 24 January 1966, *Oregon* stn 6404. 1 ♀, USNM, W of Lighthouse Reef, 262 m, 23 January 1967, *Oregon* stn 6403. 6 ♂ 7 ♀, USNM, W of Lighthouse Reef, 183 m, 24 January 1967, *Oregon* stn 6405.

NICARAGUA—1 ♀, USNM, NE of Puerto Cabezas, 183-219 m, 21 May 1962, *Oregon* stn 3568. 1 ♀, USNM, NE of Puerto Cabezas, 274-293 m, 21 May 1962, *Oregon* stn 3566. 11 ♂ 23 ♀, USNM, 190 m, off La Barra de Río Grande, 5 February 1967, *Oregon* stn 6426. 7 ♂ 3 ♀, USNM, off La Barra de Río Grande, 176-110 m, 5 February 1967, *Oregon* stn 6427. 18 ♂ 10 ♀, USNM, NE of Islas del Maíz, 119 m, 5 February 1967, *Oregon* stn 6432. 23 ♂ 18 ♀, USNM, NE of Islas del Maíz, 192-198 m, 7 February 1967, *Oregon* stn 6448. 5 ♀, USNM, NE of Islas del Maíz, 198-201 m, 7 February 1967, *Oregon* stn 6447.

PANAMA—1 ♂, USNM, off Coclé del Norte, 137 m, 29 May 1962, *Oregon* stn 3587.

VENEZUELA—2 ♂ 1 ♀, USNM, off Golfo de Venezuela, 201 m, 26 September 1963, *Oregon* stn 4398. 1 ♀, USNM, off Puerto Cumarebo, 161-187 m, 27 July 1968, *Pillsbury* stn 757. 2 ♂ 3 ♀, USNM, E of Pen de Paraguaná, 915 m, 4 October 1963, *Oregon* stn 4416. 1 ♂, USNM, off La Guaira, 97 m, 13 October 1963, *Oregon* stn 4459. 1 ♂ 1 ♀, USNM, off La Guaira, 97 m, 13 October 1963, *Oregon* stn 4461. 2 ♂, UMML, W of I La Tortuga, 68-60 m, 22 July 1968, *Pillsbury* stn 734. 26 ♂ 11 ♀, USNM, off Cabo Cordera, 60-73 m, 22 July 1968, *Pillsbury* stn 737. 6 ♂ 3 ♀, USNM, NE of Islas Los Testigos, 585-439 m, 24 September 1964, *Oregon* stn 5039. 2 ♀, USNM, NE of Islas Los Testigos, 128-119 m, 24 September 1964, *Oregon* stn 5040.

BRAZIL—Amapá: 1 ♂ 1 ♀, USNM, mouths of the Amazon River, 229 m, 17 November 1957, *Oregon* stn 2080. Maranhão: 1 ♀, USNM, off São Luis, 183 m, 9 March 1963, *Oregon* stn 4225. São Paulo: 1 ♂ 1 ♀, IOUSP, SSE of I de São Sebastião, 156-152 m, 3 July 1971, *Prof. W. Besnard* stn 1471. 4 ♂ 2 ♀, USNM-MP, SE of Quemado Grande I, 97-100 m, 11 December 1961, *Calypso* stn 138.

Description.–Body robust (Figure 56), integument firm, mostly glabrous, but carapace with rather long densely set setae on rostrum above adrostral carina; patch of minute setae extending from orbital margin to base of epigastric tooth; and elongate patch of sparsely set setae below hepatic sulcus.

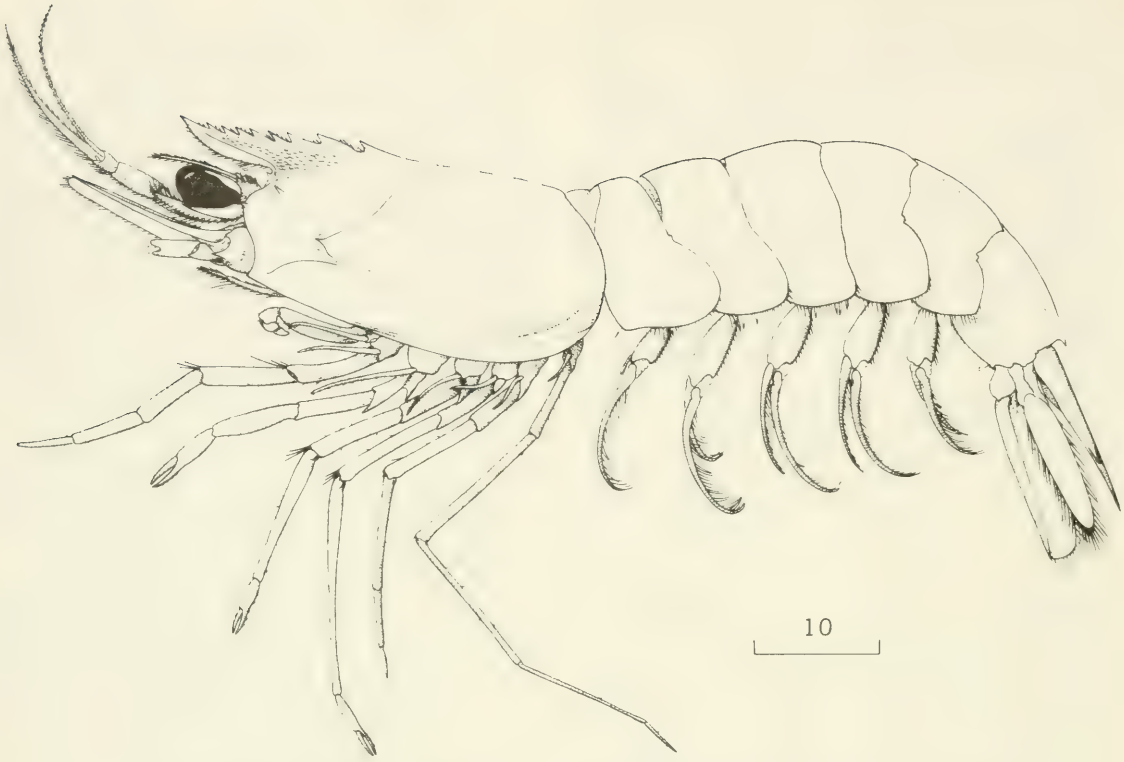

FIGURE 56.—*Mesopenaeus tropicalis*, ♀ 23.5 mm cl, east of Cayos de Albuquerque, western Caribbean. Lateral view.

Rostrum rather short, its length not exceeding 0.4 that of carapace, reaching, at most, base of second antennular article, straight or slightly tilted upward, moderately high, its ventral margin strongly convex, often with subapical concavity giving rise to saber shaped tip. Rostral plus epigastric teeth 7-10, mode 8 (percentage distribution in North America: 7-2, 8-60, 9-36, 10-2, $N = 100$; percentage distribution in South America: 7-4, 8-80, 9-15, 10-1, $N = 100$); teeth long and sharp; usually third rostral tooth, sometimes second, at level of orbital margin. Adrostral carina sharp, extending from orbital margin to ultimate tooth; postrostral carina low, short, extending only to level of cervical sulcus. Orbital spine with broad base, short but sharp; postorbital spine longest of lateral spines on carapace; antennal spine moderately long, and hepatic spine about same length. Cervical sulcus deep, gently sinuous, extending almost to, but not crossing, postrostral carina, ending at about 0.55 cl; hepatic sulcus almost horizontal posteriorly, turning anteroventrally in broad arc below hepatic spine, and nearly reaching anterior margin of carapace.

Eye (Figure 57) with basal article produced distomesially into densely pubescent, elongate, narrow scale; ocular peduncle short; cornea rather broad, greatest diameter about 1.8 times that of base of ocular peduncle, its proximal margin strongly slanting posterolaterally.

Mandibular palp (Figure 58*A*) broad, distal article almost as long as proximal, and armed with unique distomesial series of hooks. First maxilliped as illustrated (Figure 58*B*); rudimentary arthrobranchia on articular membrane (Figure 58*Bc-c*^{1}). Antennular peduncle length about 0.6 cl; prosartema long, reaching as far as midlength of second antennular article; stylocerite long, spiculiform distally, its length about 0.7 of distance between its base and that of distolateral spine; latter rather long, very slender, and sharp. Ventral antennular flagellum typically depressed, slightly shorter than subcylindrical dorsal flagellum. Flagella longer in North American than in West Indian, Central American, and South American populations (Figure 59). Ratio of

length of dorsal flagellum to length of carapace in North American shrimp ranging from about 1.15 in 10-mm cl individuals to about 0.95 in 23-mm cl shrimp. In Bahamian and southern populations, ratio decreasing from about 0.95 in shrimp 10 mm cl to about 0.6 in shrimp 24 mm cl. Scaphocerite not reaching distal margin of antennular peduncle or exceeding it by as much as 0.1 of its own length; lateral rib ending distally in long spine, usually extending to level of distal margin of lamella; antennal flagellum at least 3.5 times total length of shrimp: 110-mm tl female with flagellum 385 mm long (measurements taken by me of specimen caught south of Great Inagua, Bahama Islands, in 311 m, at *Oregon II* stn 10849). Third maxilliped usually exceeding antennular peduncle by length of dactyl, occasionally surpassing it by length of dactyl and as much as 0.2 that of propodus; length of dactyl about 0.75 that of propodus.

First pereopod, stoutest of five, reaching at most distal end of carpocerite. Second pereopod surpassing carpocerite by length of dactyl or by entire length of propodus. Third pereopod exceeding antennular peduncle by 0.6 to entire length of propodus. Fourth pereopod overreaching carpocerite by 0.5 or more length of dactyl. Fifth pereopod, longest of five, exceeding antennular peduncle by length of dactyl or by latter and as much as 0.2 length of propodus. Order of pereopods in terms of their maximal anterior extensions: first and fourth, second, third and fifth. First pereopod with long, strongly pointed spines on basis and ischium; second pereopod with long sharp spine on basis. In female, coxa of third pereopod produced into plate extending mesially, then uniquely folded ventrolaterally; coxa of fourth pereopod produced in strong plate resembling head of bird, "beak" consisting of long, sharp spiniform projection directed posteriorly, entire plate curving around lateral horn on plate of sternite XIII; coxa of fifth pereopod bearing short plate produced anteromesially in blunt projection. In male, coxa of fourth pereopod with short plate bearing small anterior tooth; fifth pereopod with large subtriangular tooth on anterior margin.

Abdomen with sharp, high, middorsal carina from third to sixth somites; low, rounded, sometimes barely perceptible carina on second somite in larger specimens; posterodorsal margin of third through fifth somites with median incision; sixth somite with small, sharp spine at posterior end of carina, and pair of small spines posteroventrally. Telson with median sulcus deep anteriorly and penetrated posteriorly by longitud-

FIGURE 58.—*Mesopenaeus tropicalis*, ♀ 20 mm cl, west of Light House Reef, Belize. *A*, Mandible. *B*, First maxilliped. *c*, Arthrobranchia. c^1, Enlargement of *c* (all from left side).

FIGURE 57.—*Mesopenaeus tropicalis*, ♀ 25 mm cl, off Key Largo, Fla. Eye.

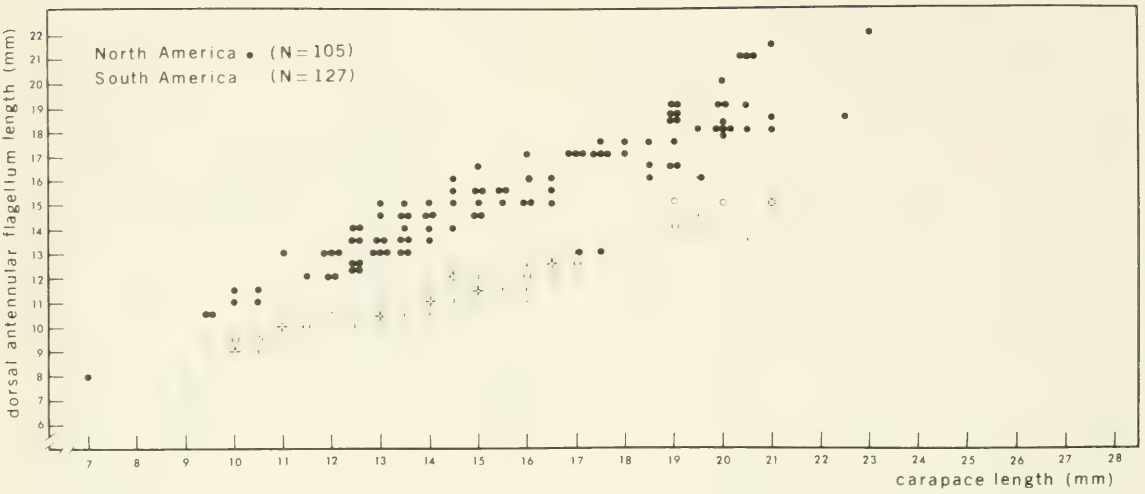

FIGURE 59.—*Mesopenaeus tropicalis*. Relationship between length of dorsal antennular flagellum and carapace length.

inal elevation merging with convex terminal portion; latter moderately long, its length 4-5 times basal width; lateral spines short, 0.9-1.4 times basal width of terminal portion; mesial ramus of uropod reaching tip of telson or overreaching it by no more than 0.1 of its own length; lateral ramus surpassing mesial ramus by 0.1-0.2 of its own length, and bearing small, terminal, distolateral spine.

Petasma (Figure 60*A, B*) cincinnulate along proximal 0.7 of median line and with terminal margin lacking spinules, often minutely rugose across ventromedian lobule; distal portion of ventromedian lobule thick, flexible, folded, its mesial portion strongly excavate ventrally, and overlying its shorter lateral portion; latter produced laterally into process resembling bird head in silhouette, dorsolateral lobule with heavy rib curved in hooklike terminal portion lying against ventral surface of process; inner surface of dorsolateral lobule studded with minute setae mesially and bearing proximolateral row of long setae; corresponding, but shorter, row of long setae on outer surface. Ventral costa reaching distally as far as, or slightly overreaching, row of cincinnuli, trending dorsally, and bearing flexible subrectangular, marginal flap, extending horizontally almost perpendicular to costa.

Appendix masculina (Figure 60*C, D*) very elongate, convex dorsally, deeply channeled ventrally, its proximal part produced laterally into rounded, ventrally turned lobe; distal part tapering, its tip twisted mesiad, mesial surface deeply concave, and armed with densely set, relatively long setae on proximolateral border, short setae on borders of concavity, and tuft of long setae apically. Appendix interna almost as long as appendix masculina, broad, subelliptical, bearing lateral rib, abutting corresponding border of appendix masculina, and armed with tuft of long setae on distolateral border, and very short setae on mesial border. Basal sclerite obliquely crossed by heavy ridge separating deep proximal concavity from anterior depressed area, and with its ventrolateral spur proximally rounded and strongly attenuate distally.

Thelycum (Figure 61) with paired short, blunt, cushionlike protuberances on flexible anterior part of sternite XIV, contiguous to ventrally raised, heavily sclerotized posterior shield; free border of shield sharp or thickened, and varying from slightly concave to produced into anteromedian, minute spine. Median plate of sternite XIII divided by median longitudinal incision into paired rounded to subrectangular lobes overhanging sternite XIV, each bearing blunt horn anterolaterally. Sternite XII with paired blunt, distally flattened projections overhanging sternite XIII.

Photophores.–Observations by me on freshly collected specimens demonstrated that this species, like *H. affinis* and *H. debilis,* bears photophores, which are arranged as follows: one adjacent to the base of the podobranchia of both the third maxilliped and fourth pereopod, and a pair on the anterior part of the sternum from the second through

the sixth abdominal somites, immediately posterior to the transverse ridge of the preceding segment. The seven pairs of photophores consist of a yellow conical portion and a red lens.

Color.–Body translucent salmon with obliquely vertical, deep yellow stripes, and milky white patches of various sizes on carapace. Rostrum yellow from second rostral tooth to apex, epigastric and first rostral teeth salmon. Carapace with three anterior stripes resembling chevron: anteriormost short, arched, extending from near base of orbital spine posterodorsally to below first rostral tooth; second extending almost from base of postorbital spine to posterior base of epigastric tooth; third posteriorly flanking cervical sulcus, and broadening on middorsum, forming diamond-shaped mark. Additional posterior stripe on carapace narrow on middorsum, broadening rapidly anteroventrally, and then narrowing again, forming band along dorsal part of branchiostegite. White patches on carapace very conspicuous: anterior one subcircular, situated on depression below hepatic spine; second oblong, lying ventral to hepatic sulcus; posteriormost ovate and large, almost covering entire branchiostegite. First abdominal somite with yellow spot immediately anterior to posterolateral hinge, remaining five somites with broad, uniformly wide yellow stripe extending from anterior half of middorsum posteroventrally to lateral hinge, except stripe on sixth reaching posteroventral extremity of pleuron; sixth somite also with short posterodorsal yellow stripe extending from dorsum to lateral base of telson; midventral part of pleura of anterior five somites with deep salmon spot, sixth somite with deep salmon patch on anteroventral part of pleuron. Telson salmon, with median sulcus yellow; uropodal rami bearing broad transverse band across midlength. Antennulae and antennae deep salmon, darker on basicerite of antenna and on adjacent anteroventral portion of carapace. Thoracic sternites, first and second maxillipeds, and proximal podomeres (including merus) of third maxilliped and pereopods pale salmon; distal podomeres deep salmon except for narrow milky white longitudinal band. Basis of pleopods deep salmon preaxially with lateral part milky white; endopods and exopods whitish with orange line along midlength; ventral surface of

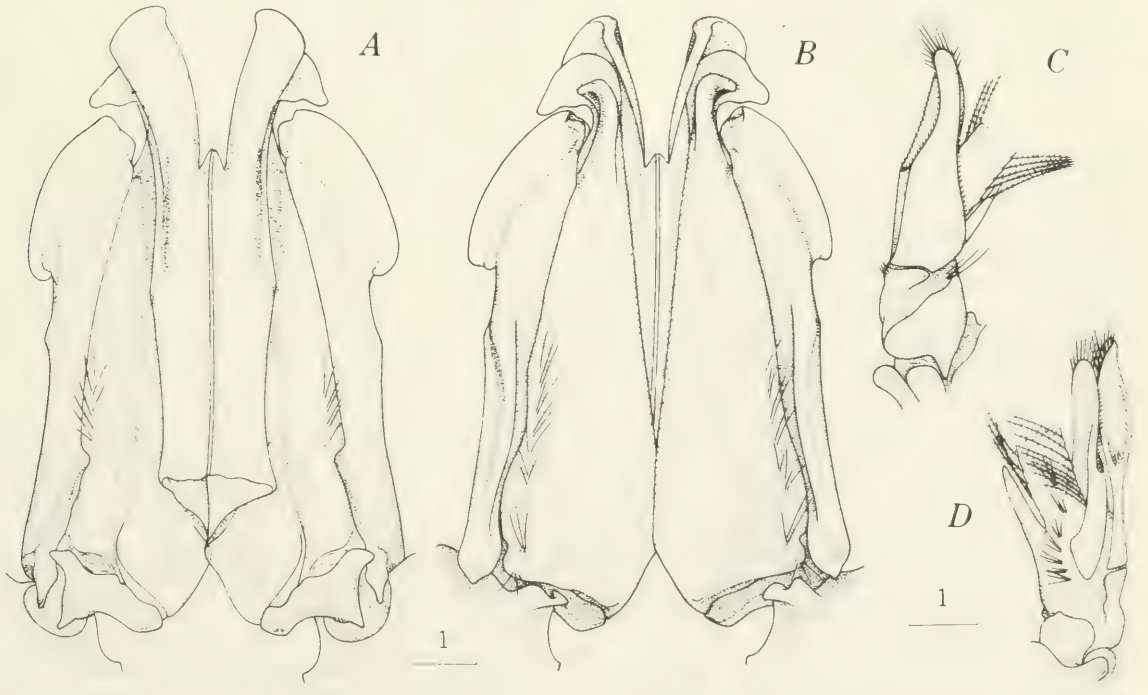

FIGURE 60.—*Mesopenaeus tropicalis*, ♀ 17.5 mm cl, east of Cayos de Albuquerque, western Caribbean. *A*, Petasma, dorsal view. *B*, Ventral view. *C*, Right appendices masculina and interna, dorsal view. *D*, Ventromesial view.

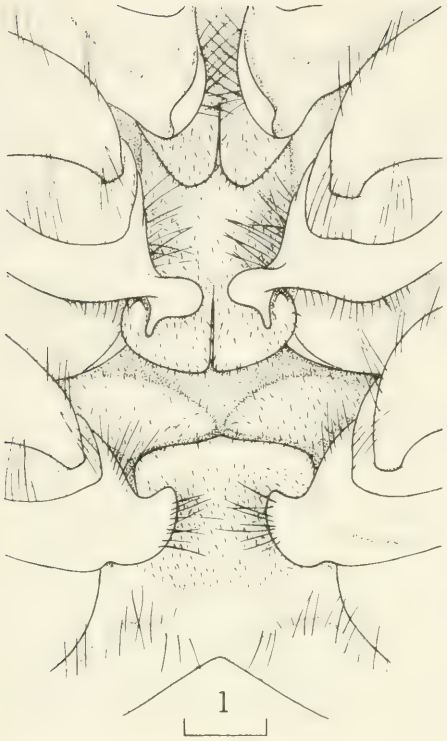

FIGURE 61.—*Mesopenaeus tropicalis,* ♀ 25.5 mm cl, east of Cayos de Albuquerque, western Caribbean. Thelycum, ventral view.

abdomen with orange transverse rib at posterior margin of sternites, interrupting overall translucent salmon.

Although the color pattern described is altered with the expansion and contraction of the chromatophores, this basic arrangement of colors was usually recognizable in all specimens examined by me. However, according to Iwai (1973), this species exhibits an overall red in Brazilian waters.

Maximum size.–Males: 20.5 mm cl; females: 28 mm cl.

Geographic and bathymetric ranges.–Northeast of Cape Lookout, N.C. (34°43′N, 76°40′W), to the Straits of Florida, and into the Gulf of Mexico to Alabama. Also off the Bahamas, through the Caribbean, and along the Atlantic coast of South America as far as Rio Grande do Sul (Figure 34). The record from Rio Grande do Sul (34°00′S) is from Iwai (1973). This species occurs at depths between 30 and 915 m (Figure 9), thus from relatively shallow waters (where it is infrequent) on the continental shelf to the upper zone of the continental slope. This bathymetric range is not peculiar to *M. tropicalis,* but is also exhibited by various other penaeoids. The single record of the shrimp from northeast of Cape Catoche, and its apparent absence in the Gulf of Mexico from Mississippi to northern Yucatán, suggest inadequate sampling in the region. Its presence on the continental slope, even if only in the shallower zone, where no barriers prevent its dispersion, also favors this conclusion.

According to the limited data at my disposal, in the warm temperate waters of North America this species tends to remain on the continental shelf, where 85% of the samples examined by me were caught; in contrast, off the Bahamas and to the south, it seems to be more abundant off the shelf edge, where 76% of the samples were taken. In neither region do the animals appear to exhibit a seasonal migration, moving from warmer waters of the shelf to greater depth in late fall and returning in the spring.

Affinities.–Mesopenaeus tropicalis, ths sole member of the genus, differs strikingly from the other solenocerids occurring in the western Atlantic in possessing antennular flagella which are dissimilar in shape, the dorsal one subcylindrical and the ventral depressed.

Variations in the relative length of the antennular flagella were pointed out by Lindner and Anderson (1941). I have confirmed their observations and, in addition, have found that the range of variations in North American populations is different from that in populations occurring from the Bahamas to Brazil, the former having longer flagella than the latter. Noteworthy is the parallelism that exists in the relative length of the antennular flagella between *Mesopenaeus tropicalis* and two closely related allopatric species of the genus *Solenocera.* Like the northern population of *M. tropicalis, S. vioscai,* a North American species, possesses longer flagella than does *S. acuminata,* which occurs from the Bahamas to Brazil (Pérez Farfante and Bullis 1973). A similar tendency was observed by Pérez Farfante and Bullis in *S. atlantidis,* the northern populations of which tend to have longer flagella than do those from the Bahamas southward. The thelycum of *M. tropicalis* also exhibits considerable variation, even within a single population, the shield of sternite XIV varying from flat with the anterior

margin bladelike, to deeply excavated on the median portion, and with the anterior margin elevated in a strong ridge; in addition, this margin ranges from bearing a minute anteromedian spine to being concave. Furthermore, the anterolateral protuberances of sternite XIII may be low or rather strongly raised.

Spermatophore.–Compound spermatophore consisting of slender, laterally compressed geminate body continuous with broad anterior lobes, bearing lateral wings, and produced posterolaterally in relatively narrow flanges (Figure 62).

Thick opaque ventral wall and lateral wall of each spermatophore (Figure 63*A*) extending anteriorly forming ventral portion of anterior lobe; lateral wall, opaque anteriorly, translucent posteriorly, bearing fleshy wing; dorsomesial wall (Figure 63*B*) mostly translucent but thickened mesially, continuous with dorsomesial portion of anterior lobe, and extending posteromesially beyond fundus of sac, there joining flange, and giving rise to pocketlike caudal projection. Anterior lobe forming obliquely truncate collar opening laterally and through posterior slit, with ventrolateral surface subrectangular, and dorsomesial surface elongate trapezoidal, broadest laterally. Wing flexible (lacking heavily sclerotized supporting structures), bearing rounded lobe anteriorly. Flange extending from about midlength of sac around posterolateral margin, bearing anteriorly cornified, reniform projection, and produced laterally in roughly semicircular flap. Spermatophore supported by strong C-shaped armature, its mesial part fused to dorsomesial wall and its anterior arm extending across and supporting ventral wall, with lateral extremity forked: anterior branch forming foliaceous process, directed dorsally, facing posterior slit of anterior lobe; posterior branch spirally twisted and located just cephalic to reniform projection of flange. Dorsal plate elongate ovate, extending from base of wing to posterior margin of flange.

Compound spermatophore attached to female with anterior lobes on sternite XII, their elongate lateral openings lying close to gonopores; angles formed by anterior lobes and wings embracing posterior corners of coxal plates of third pereopods; wings extending laterally, attached to sternite XIII, pressing against marginal ridge of XII. Posterior part of geminate body affixed by dorsal plates to shieldlike posterior plate of sternite XIV, elevated (ventrally) well above level of anterior

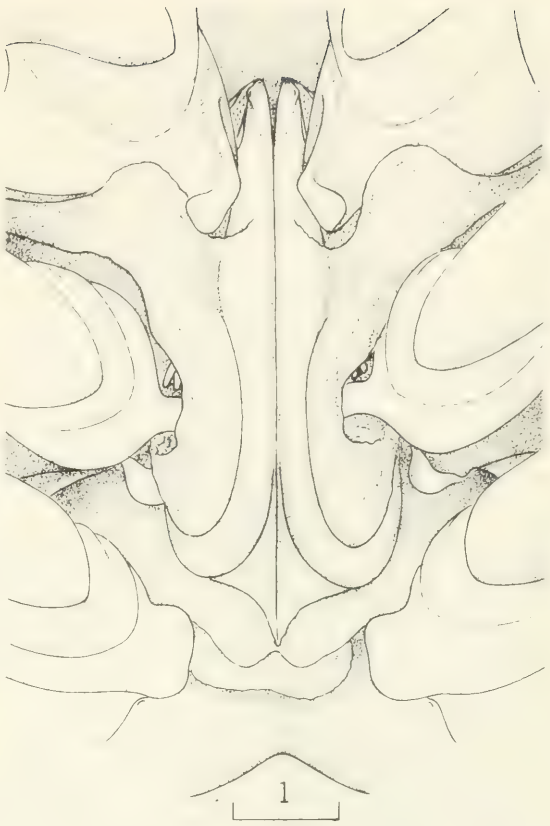

FIGURE 62.—*Mesopenaeus tropicalis*. Compound spermatophore attached to female, ♀ 19.5 mm cl, off Gulf Beach, Fla. (setae omitted).

lobes, thus geminate body directed anterodorsally. Posterior parts of flanges sloping posterodorsally, lateral parts attached to sternite XIV, and reniform projections lying near coxae of fourth pereopods. Finally, foliaceous processes meeting on middorsal line, whereas spirally turned branches of C-shaped armature (diverging from bases of foliaceous processes) projecting laterally.

I have observed sperm masses protruding from the sperm sacs into the cavity of the respective anterior lobe, from which the sperm must be dispersed into the surrounding water adjacent to the female gonopores. A complete compound spermatophore detached by me from an impregnated female was found to lack sperm masses, suggesting that the sperm had been freed while the intact spermatophore was still anchored to the animal; furthermore, there was no trace of such masses on

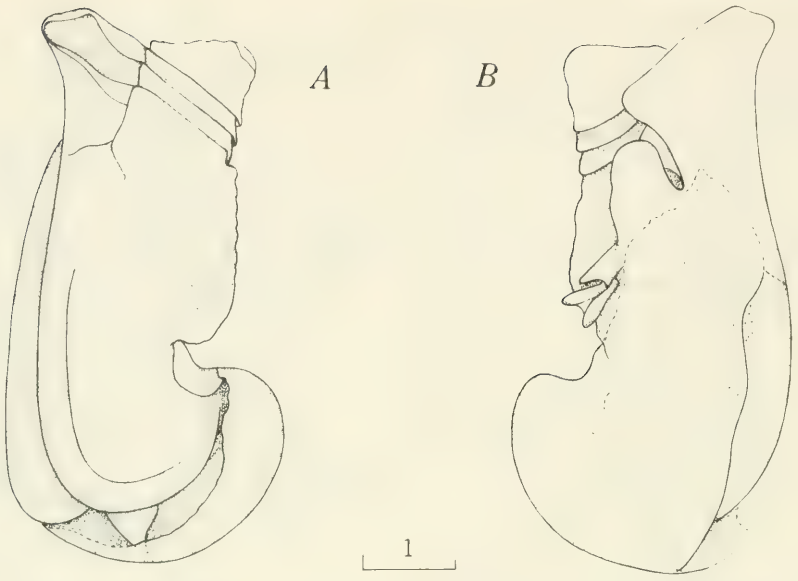

FIGURE 63.—*Mesopenaeus tropicalis*, ♂ 19 mm cl, south of Great Inagua, Bahama Islands. *A*, Left spermatophore dissected from terminal ampulla (wing slightly displaced), ventrolateral view. *B*, Dorsomesial view (dorsal plate removed).

the thelycum. Unlike the release of the sperm masses in certain members of the subgenus *Litopenaeus* (genus *Penaeus*) the sperm appears to be liberated in *M. tropicalis* without a rupture of the spermatophore.

Three females with spermatophores attached were examined by me. The smallest of these specimens, 12 mm cl, was caught off Savannah, Ga., at *Silver Bay* stn 3658. The other two were 19.5 mm cl, and one was taken south of St Vincent Island at *Oregon* stn 896 and the other off Gulf Beach at *Oregon* stn 1254, both localities off northwestern Florida.

Remarks.–In his original brief diagnosis of *Parartemesia tropicalis,* Bouvier (1905b) stated that the species is from the "mer des Antilles," where it had been collected between 80 and 175 fm (146 and 320 m), during a cruise of the *Blake;* he cited neither the number of specimens he had examined nor the locality where they had been found. Later, he (1906b) mentioned the same shrimp (including it among the species of the genus *Haliporus* found in the tropical subtropical Atlantic) as occurring in the "Antilles." However, A. Milne Edwards and Bouvier (1909)—in a rather detailed account of various morphological features of the female of the species, including the thelycum—referred to the same specimen (17.5 mm cl, about 74 mm tl), as the "type," and added the following information: "Habitat, . . .—Blake: Florida Bank, lat. N. 26° 31′, long. O. 85° 03′, 119 brasses.—Le type femelle décrit plus haut." Furthermore, on plate 3, eight figures are explicitly identified as parts of the "type." A. Milne Edwards and Bouvier also recorded and illustrated a smaller female, "25 à 30 mm de longeur" (5.5 mm cl, about 27 mm tl), from Barbados taken in 76 fm (139 m) which, according to a label dated 1907, in Bouvier's handwriting, is a "cotype juvenile," evidently thus designated during the course of the investigations published 2 yr later. The minimum depth of the bathymetric range (80-175 fm) originally given for the species is only slightly greater than that at which the small female was collected, but the maximum depth is considerably deeper than that reported for the larger female, suggesting that the authors had examined additional specimens. Of the material first studied by Bouvier, these two females are the only specimens of this species known to have been taken during cruises of the *Blake* and, furthermore, the small one was identified by Bouvier on a piece of paper accompanying the specimen in the bottle as *Parartemesia tropicalis,* i.e., within the genus proposed in 1905. Consequently, I am convinced that

these two specimens are part of the syntypic series. Inasmuch as the larger female was treated as the type by A. Milne Edwards and Bouvier, I am furthering the latter authors' intent by designating it the lectotype of *Parartemesia tropicalis* [=*Mesopenaeus tropicalis*], and the small female is, therefore, a paralectotype.

The type-locality of *H. tropicalis* is uncertain. A. Milne Edwards and Bouvier (1909) copied the coordinates of *Blake* stn 50 from the label enclosed in the jar with the specimen; I have examined this label and confirmed their data. However, the locality corresponding to those coordinates is beyond the 1,500-fm (2,744-m) contour, and thus considerably deeper than the greatest depths otherwise recorded for this shrimp, a species that penetrates only the shallower portion of the upper slope. Prior to the publication of A. Milne Edwards and Bouvier, the coordinates and depth of *Blake* stn 50 were recorded, in a serial list of *Blake* stations (Anonymous 1879), as follows: 26°31′N, 85°53′W, 119 fm (218 m). Later, S. Smith (1889) quoted the latter data, noting that "The position or depth must be wrong as there are 1700 fm (3109 m) there, perhaps 28°31′." S. Smith's suggestion concerning the latitude was perhaps based on that of the three previous *Blake* stations, which were 28°42′00″N, 28°47′30″N, and 28°51′30″N; however, these are at longitudes greater than 88°W, situated off the Delta of the Mississippi River, and thus far from Florida. The confusion regarding the location of station 50 is even greater, because the name "Florida Bank" is not found on American hydrographic charts, although it can be deduced that A. Milne Edwards and Bouvier referred to West Florida Shelf, the edge of which lies just east of where, according to the label, the specimen was obtained. It seems to me that the type-locality of this species will remain indeterminable.

Under the name *Solenocera weymouthi,* Lindner and Anderson (1941) presented an excellent description of *M. tropicalis.* Two of their statements seem to be in need of modification: only the ventral antennular flagellum is flattened (but not canaliculate), the dorsal one being subflagelliform. The locality given for the allotype is in error. W. L. Schmitt kindly allowed me to examine his logbook of the collections made off the Dry Tortugas in 1932, the time at which the specimen was collected. His records show that "boat sta 74," the locality in question, corresponds to the *Anton Dohrn* trawl haul made 14 miles (22.5 km) south of the Dry Tortugas in 60 fm (110 m) on 5 August 1932. The data given by Lindner and Anderson are those for *Anton Dohrn* station 71, made the same day but, as they quoted, 19.5 miles (31.4 km) south of the Dry Tortugas at 190-280 fm (347.5-512 m).

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SMALL-SCALE MOVEMENTS OF ALBACORE, *THUNNUS ALALUNGA*, IN RELATION TO OCEAN FEATURES AS INDICATED BY ULTRASONIC TRACKING AND OCEANOGRAPHIC SAMPLING

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ABSTRACT

Studies with ultrasonic tracking techniques and oceanographic sampling demonstrated that oceanographic conditions play an important role in the local concentrations and movements of albacore, *Thunnus alalunga*, in U.S. coastal waters. Albacore show a tendency to congregate in the vicinity of coastal upwelling fronts, presumably to feed. They move away from the immediate area when upwelling ceases and the upwelling front is no longer present at the surface. The movements of albacore also appear to be related to the distribution of sea surface temperature, with fish spending little time in water with surface temperatures cooler than 15.0°C.

The average swimming speed for three fish tracked between 27.8 and 50 h was 1.6 knots (82.4 cm/s) with each fish exhibiting slightly faster swimming speeds during hours of daylight than during hours of darkness.

The albacore, *Thunnus alalunga* (Bonnaterre), is widely distributed in the Pacific Ocean. The single subpopulation which is found in the North Pacific (Otsu 1960) supports important surface commercial fisheries in coastal waters off North America and Japan and subsurface fisheries in the central temperate Pacific. The species is also highly prized by U.S. recreational fishermen. Passive tagging methods have been used to study large-scale migratory patterns of albacore in the North Pacific (Ganssle and Clemens 1953; Otsu 1960; Clemens 1961, 1963; Otsu and Uchida 1963; Laurs and Nishimoto[4]); however, information on small-scale movements is scant.

In order to examine the small-scale movements of schools of albacore and evaluate the effects that oceanographic conditions may have on the local concentrations and movements of albacore in coastal waters off the United States, studies were conducted with ultrasonic tracking techniques and oceanographic sampling.

Tracking the movements of animals to which ultrasonic transmitters have been attached is a technique that has been developed over the past two decades. This valuable technique has gained such wide application in recent studies of marine fishes and crustacea that it is more convenient to cite a bibliographic source (Stasko 1975) than to cite individual references.

METHODS

In the course of acoustic tracking studies, environmental data commonly have been collected for correlation with observed movements of the animal. At times, small auxiliary craft have been used for this purpose in support of the vessel doing the tracking, but usually the collection of environmental data has been done entirely from aboard the tracking vessel, necessarily limiting measurements to the ship's track. This study represents a significant expansion of supportive environmental data acquisition: for the first time a major oceanographic research vessel and an aircraft were coordinated with acoustic tracking of fish. The ultrasonic tracking experiment involved the use of the commercial albacore fishing baitboat *Linda* on charter to the American Fishermen's Research Foundation, the National Marine Fisheries Service (NMFS) RV *David Starr Jordan,* and a Coast Guard aircraft equipped with sea surface temperature measuring equipment.

Capture, Handling, and Tagging of Albacore

The capture of fish, tagging with ultrasonic

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transmitters, and tracking of the fish were done aboard *Linda* by three NMFS scientists with assistance from the crew of *Linda*. Albacore ranging in size from 74 to 87 cm fork length with estimated weights of 8.2 to 13.6 kg were caught on hook and line baited with anchovy. The fish was played an average of 5 min before being brought on board by dip net. Without removing it from the net, the fish to be tagged was placed on its side on a plastic covered foam measuring pad on the deck where it was measured to the nearest lower centimeter and the transmitter was attached. A wet burlap bag was placed over its head to keep the fish calm. No anesthetic was used.

The ultrasonic transmitter was attached to the back of the fish, immediately in front of the second dorsal fin, with two sutures through the skin and muscle tissue in that area. Upon completion of tagging, fish were immediately replaced in the water. Total elapsed time for fish out of water was between 1 and 1½ min. Within 2 to 4 s after being released, each tagged fish was observed righting itself and actively swimming downward and out of sight. One fish was tracked at a time. The three fish tracked longer than 24 h were tagged in the manner described above. Several fish tracked for shorter periods early in the cruise were tagged by inserting the transmitter into the stomach through the mouth. This latter method was abandoned when it appeared that acoustic signal attenuation caused by internal implacement was resulting in an inadequate receiving range.

Tracking Equipment

The transmitter tags and hydrophone used were built by the Northwest and Alaska Fisheries Center, Seattle, Wash. The tags were cylindrical measuring 8.2 by 1.9 cm, weighing 67 g in air and 43 g in water, and emitted a 45 or 50 kHz signal at a pulse rate of 120 pulses/min. Acoustic source level of the tag was 63 dB (reference to 1 μbar at 1 m in fresh water).

The hydrophone was a tuned 6-element array (sensitivity - 69 dB, reference to 1 μbar at 1 m) with a beam width of 20° horizontally and 40° vertically at the 3-dB point. This was attached to the lower end of a 3-cm aluminum pipe, bracketed to the starboard rail amidship of the tracking vessel. A geared electric motor at the top of the pipe rotated the hydrophone, which was remotely controlled from the tracking station in the wheelhouse. Signals picked up by the hydrophone were fed into a Lawson VLF-1[5] superheterodyne receiver.

Tracking Procedure

With the hydrophone remote-control unit installed in the pilothouse of *Linda* alongside the engine and steering controls and the receiver placed about 2 m away, one person was able to operate the tracking system and control the vessel simultaneously. Directing the hydrophone for maximum signal, the operator moved the vessel on that heading until satisfied, on a basis of signal strength, with his proximity to the fish. The receiving range varied widely according to sea state, but on the average *Linda* was kept an estimated 500 m from the tagged fish. The fish moved continuously and so, consequently, did the vessel, but vessel speed of more than 2 knots was seldom necessary to keep up with the fish. Position of the tracking vessel was determined approximately once an hour and was taken also to represent the position of the fish at that time. Most of the navigation for *Linda* was done by the nearby *David Starr Jordan*, with a combination of Loran, radar, and Omega systems.

Oceanographic Observations Made From Ship

Detailed oceanographic observations were made aboard *David Starr Jordan* in support of the ultrasonic tracking experiments. These included continuous monitoring of surface temperature and salinity and measurements of subsurface temperature and salinity at selected stations. Observations were also made to evaluate biological factors of the marine environment. These included continuous monitoring at the surface and subsurface measurements at selected stations of chlorophyll a by fluorometric techniques (Holm-Hansen et al. 1965), measurements of primary productivity by ^{14}C methods (Owen and Zeitzschel 1970), and estimates of the standing stocks of potential albacore food organisms.

The estimates of potential albacore forage were derived from hauls made with a 1.8-m Isaacs-Kidd midwater trawl (IKMT) lined with a 58-mm mesh. The hauls were taken during hours of darkness

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

from the surface to a depth of approximately 175 m at a ship speed of about 5 knots. The volumes of water strained were estimated from data obtained by a TSK[6] depth-distance recorder mounted in the mouth of the trawl. The Formalin-preserved IKMT catches were sorted into several categories of fishes, cephalopods, crustaceans, and other animals, and the displacement volume of each of these kinds of animals was measured and standardized in ml/1,000 m^3 of water filtered for each haul. The standardized values of 1) larval and juvenile fishes, 2) epipelagic fishes, 3) cephalopods, and 4) crustaceans were summed for each haul and collectively regarded as potential albacore forage. Analysis of stomach contents of albacore has shown that these categories of organisms are important in the diet of albacore (Pinkas et al. 1971) in this area.

Oceanographic Observations Made by Aircraft

A Coast Guard aircraft equipped with a Barnes PRT-5 infrared radiometer made measurements of sea surface temperature for evaluation of the small-scale features and changes in the distribution of sea surface temperature.

RESULTS AND DISCUSSION

Six albacore were tagged and tracked with ultrasonic equipment for periods ranging from about 2 to 50 h and distances ranging from 6.5 to 150.7 km (3.5 to 81.3 nmi). Results will be presented for fish numbers 4, 5, and 6, which were tracked for 27.8, 41.4, and 50.0 h, respectively. There are too few data for discussion for fish numbers 1, 2, and 3 because of the short periods that the fish were tracked. A summary of the tracking date and time, tagging location, distance tracked, and fork length of fish for fish numbers 4, 5, and 6 is given in Table 1.

Tagged fish rejoined untagged albacore after being returned to the water, and tended to remain in their company. Surface "boils" characteristic of albacore were frequently sighted close by *Linda*, and approximately 30 fish of the same general size as fish tagged with ultrasonic transmitters were caught by the crew while tracking was in progress. Also, one tagged fish "lost" the previous day was heard intermittently over a 4-h period during the track that followed. We were able to distinguish between the two fish because of slightly different signals from the tags.

[6]Tsurumi Seiki Kosakusho Co., Ltd., Yokohama, Japan.

TABLE 1.—Summary of tracking date and time, fork length of albacore, location of tagging, and distance tracked.

No.	Date	Time	Fork length	Tagging location Lat.	Long.	Distance
4	8-16-72 to 8-17-72	1445 to 1845	84 cm	36°49.8'N,	122°19.1'W	41.6 nmi (77.1 km)
5	8-19-72 to 8-20-72	0715 to 2345	87 cm	36°50.3'N,	122°13.6'W	61.4 nmi (113.8 km)
6	8-25-72 to 8-27-72	1000 to 1205	85 cm	35°20.0'N,	121°22.0'W	81.3 nmi (150.7 km)

Speed of Albacore Movements

Swimming speeds for albacore were estimated from straight-line calculations using position of the tracking vessel. The average swimming speed, based on the total distance and time that the fish were tracked, for fish numbers 4, 5, and 6 was about 1.6 knots (82 cm/s). Speeds calculated from hourly ship positions for each fish ranged from 0.1 to 3.6 knots (5 to 185 cm/s). Table 2 shows the percentage of time each fish spent at various swimming speeds. There were day-night differences in the rate of movement, with fish exhibiting faster swimming speeds during hours of daylight (0500 to 1900 h) than during hours of darkness. The average speed during daylight for fish numbers 4 and 5 was 1.7 knots (88 cm/s) and for number 6 was 2.1 knots (108 cm/s). The average speed during nighttime for fish numbers 4 and 6 was 1.3 knots (67 cm/s) and for fish number 5 was 1.0 knot (51 cm/s). Table 3 gives a summary of time, distance, and mean speeds.

Moonlight also appeared to influence the rate of movement of fish number 5. This fish, which had been moving steadily at about 2.0 knots (103 cm/s) for about 3 h after moonrise and following a course about 20° west of the full moon, came to a near stop

TABLE 2.—Percent of time each albacore spent at various swimming speeds.

Speed		Fish no. 4	Fish no. 5	Fish no. 6
knots	cm/sec		Percent	
<0.5	<26	8.0	5.9	0.0
0.5-0.9	26- 46	12.0	23.5	15.8
1.0-1.4	51- 72	32.0	35.3	28.9
1.5-1.9	77- 98	24.0	11.8	15.8
2.0-2.4	103-124	16.0	17.6	28.9
2.5-2.9	129-149	4.0	2.9	0.0
3.0-3.4	154-175	0.0	2.9	10.5
3.5	175	4.0	0.0	0.0

TABLE 3.—Summary of duration and distance tracked and mean speed of albacore tracked with ultrasonic transmitters.

Item	Fish no. 4	Fish no. 5	Fish no. 6
Time tracked (h)	27.8	41.4	50.0
Distance tracked:			
nmi	41.6	61.4	81.3
km	77.1	113.8	150.7
Mean speed:			
knots	1.6	1.5	1.6
cm/s	82	77	82
bl/s[1]	0.98	0.88	0.96
Mean speed, day:[2]			
knots	1.7	1.7	2.1
cm/s	88	88	108
bl/s[1]	1.05	1.01	1.27
Mean speed, night:[3]			
knots	1.3	1.0	1.3
cm/s	67	51	67
bl/s[1]	0.80	0.59	0.79

[1]bl/s = body lengths per second.
[2]0500-1900 h.
[3]1900-0500 h.

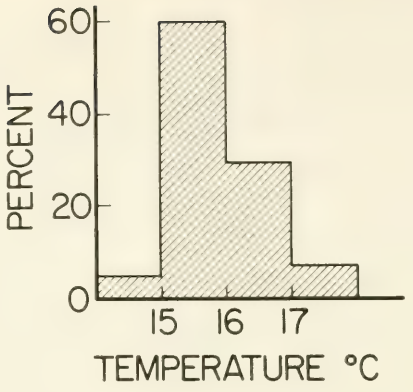

FIGURE 1.—Percent of time (hours) spent in waters of various sea surface temperature by albacore numbers 4, 5, and 6.

for nearly an hour when the moon was suddenly obscured by dense fog at about 0300 h.

The mean swimming speeds calculated from the tracking experiment are close to estimates of swimming speed derived from passive tagging results. For example, based on data given in the Japanese Fisheries Agency (1975) report, two tagged albacore, which were released in the western North Pacific and recovered in the eastern North Pacific about 3½ mo later, traveled at 1.1 knots (57 cm/s), assuming they followed a great circle route and were caught the day they arrived at the recovery location. The mean swimming speeds found in this study are slightly less than twice the calculated minimum swimming speed necessary for an 80-cm albacore to maintain hydrostatic equilibrium (Dotson 1977).

Relationship of Albacore Movements to Sea Surface Temperature

The movements of the fish tagged with ultrasonic transmitters appeared to be influenced by the distribution of sea surface temperature. Figure 1 shows the percentage of the time that fish numbers 4, 5, and 6 spent in waters of various surface temperatures. Fish number 6 spent no time in water with surface temperatures less than 15.0°C although roughly 20% of the waters 5 nmi distant on both sides of the path followed by the fish were colder than 15.0°C. Fish number 4 was in water which had surface temperatures colder than 15.0°C 12.5% of the time, while 35% of the waters 5 nmi distant on both sides of the path followed by the fish was colder than 15.0°C. Fish number 6 was in water with surface temperatures warmer than 17.0°C 22% of the time, which coincided with the percentage of area with temperatures greater than 17.0°C. Water with temperature higher than 17.0°C was not available to fish numbers 4 and 5.

These results indicate that the transmitter-tagged fish spent very little time in water with surface temperatures less than 15.0°C. This is especially evident when charts showing the tracks followed by the fish and the contoured field of sea surface temperature observed by *David Starr Jordan* at the time of tracking are examined. Figures 2, 3, and 4 show tracks followed by fish numbers 4, 5, and 6, respectively, and sea surface temperature. In these figures, temperatures less than 15.0°C, which are considered below the habitat preference for albacore (Clemens 1961), are shaded. Fish number 4 remained in the vicinity of a band of water cooler than 15.0°C for nearly the total time it was tracked, but did not appear to enter it (Figure 2). Fish number 6 traveled on a southerly course, in a corridor of warm water which was sandwiched between two wedges of cool water on 25 August, but did not enter the cool water on either side except very briefly at the start of tracking (Figure 4). When the fish passed to the south of the cool water, where there was a large area of water warmer than 15.0°C, the fish changed its direction generally to a more southwesterly course.

Relationship of Albacore Movements to Upwelling Temperature Fronts

A well-developed temperature front occurs at the boundary between cool, biologically rich

FIGURE 2.—Movements of albacore number 4 as indicated by ultrasonic tracking and contoured field of sea surface temperature in degrees Celsius. Triangles on fish track indicate hourly position. The time and date that tracking commenced is noted at the starting location and shown above and below a slash mark, respectively. The 0000 and 1200 h local time positions are also indicated. Dots show where temperature observations were made by *David Starr Jordan*. Temperatures below 15.0°C are shaded.

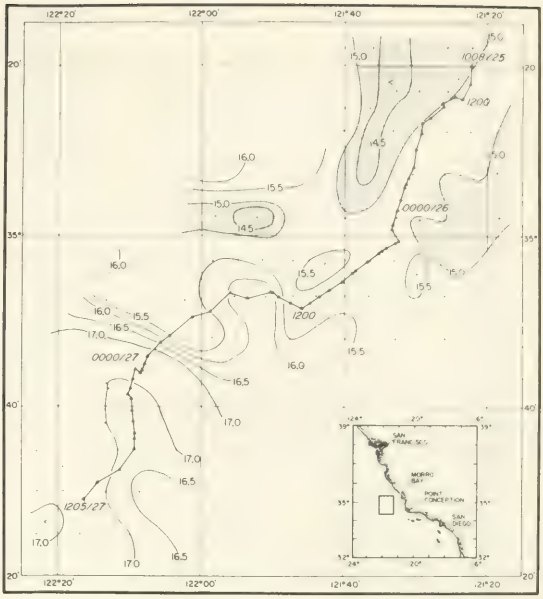

FIGURE 4.—Movements of albacore number 6 as indicated by ultrasonic tracking and contoured field of sea surface temperature in degrees Celsius. Triangles on fish track indicate hourly position. The time and date that tracking commenced is noted at the starting location and shown above and below a slash mark, respectively. The 0000 and 1200 h local time positions are also indicated. Dots show where temperature observations were made by *David Starr Jordan*. Temperatures below 15.0°C are shaded.

upwelled water and warmer, nonupwelled water (Smith 1968). The effects that an upwelling front may have on the movements of albacore were indicated during the ultrasonic tagging experiment. On 17 August, during tracking operations for fish number 4, a relatively well-developed upwelling surface temperature front was observed in the northeast portion of the tracking area. The upwelling was caused by brisk northerly winds which had been blowing for several days. The remainder of the area surveyed has a rather simple surface temperature distribution mostly within the temperature range considered as the habitat preference for albacore (Figure 2).

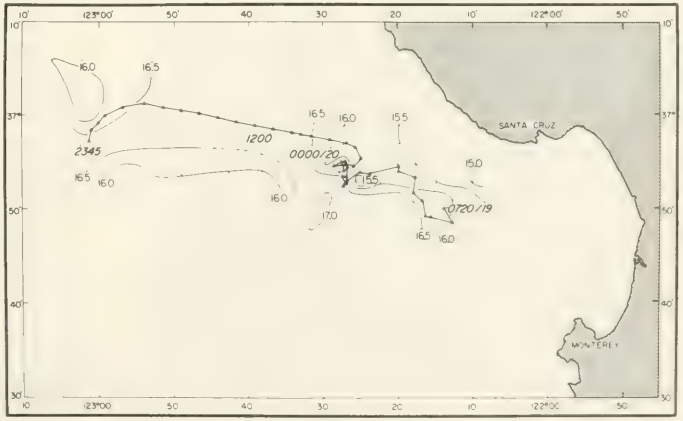

FIGURE 3.—Movements of albacore number 5 as indicated by ultrasonic tracking and contoured field of sea surface temperature in degrees Celsius. Triangles on fish track indicate hourly position. The time and date that tracking commenced is noted at the starting location and shown above and below a slash mark, respectively. The 0000 and 1200 h local time positions are also indicated. Dots show where temperature observations were made by *David Starr Jordan*.

Infrared radiation temperature measurements made during an overflight by the Coast Guard aircraft on 16 August showed that the water on the cold side of the front continued to decrease toward shore to values below 13.0°C.

Fish number 4 traveled in about an 8 × 8 nmi area on the warm side of the upwelling front and in close proximity to it for nearly the total time the fish was tracked. Subsequently, high winds and rough seas made tracking difficult and the signal from the fish was lost during hour 27 of tracking.

Fish number 5 exhibited a much different pattern of movement than did number 4 (compare Figures 2 and 3). It moved many miles from the location where it had been tagged, in a general northwesterly direction, rather than remaining in the local vicinity as fish number 4 had done.

Examination of oceanograhic data revealed that marked changes in the distribution of sea surface temperature had occurred between 17 and 19 August (compare Figures 2 and 3). Upwelling had subsided, the upwelling temperature front was no longer present on 19 August, and the temperature over much of the area had increased by about 1.5°C. The breakdown of the upwelling front and warming was due to a slackening and shifting of the winds to a westerly-southwesterly direction which allowed a thin layer of warmer offshore water to flow toward the coast.

It is presumed that the school of fish with which fish number 4 was traveling remained in the vicinity of the upwelling front to feed in the highly productive water associated with the upwelling. Measurements of chlorophyll were high in the tracking area and showed a very strong positive gradient on the cold side of the upwelling front (Figure 5). Measurements of ^{14}C uptake indicated a primary production rate integrated over the euphotic zone (0 to 36 m) of 1,511 mg C/m^2 per day. The biomass of potential albacore food organisms was also high, ranging from about 20 to 56 ml/1,000 m^3 water strained, in midwater trawl collections made at night in the nearby area where tracking took place (Table 4).

Albacore were frequently seen boiling in the area nearby the upwelling front by personnel aboard *Linda* and *David Starr Jordan*. Also, observers aboard the Coast Guard aircraft noted about 25 to 30 commercial albacore jig boats fishing immediately on the warm side of the front in water warmer than 15.0°C. High biological production in the area of the upwelling front was also indicated by large numbers of sea birds and numerous sightings of marine mammals, including blue whales and other whales.

It is possible that fish number 5 and the school it was traveling with left the immediate area where it had been tagged because food organisms were no longer concentrated there due to the breakdown of the upwelling front. This explanation is supported by the observation on 19 August of an overall reduction in the concentration of surface

FIGURE 5.—Movements of albacore number 4 as indicated by ultrasonic tracking and the distribution of surface chlorophyll in milligrams per cubic meter.

TABLE 4.—Summary of dates, times, positions, and estimates of potential albacore forage, 1972.

Fish no.	IKMT no.	Date	Time	Lat. (N)	Long. (W)	Forage biomass (ml/1,000 m^3)
4	1	15 Aug.	2200-2240	36°50'	122°14'	28.8
	2	16 Aug.	2159-2238	36°47'	122°15'	36.2
	3	17 Aug.	2137-2215	36°55'	122°24'	56.2
	4	18 Aug.	0032-0111	36°53'	122°16'	51.5
	5	18 Aug.	0130-0210	36°52'	122°19'	30.4
	6	18 Aug.	0232-0311	36°49'	122°22'	37.7
	7	18 Aug.	0352-0430	36°50'	122°11'	30.7
	8	18 Aug.	0516-0553	36°41'	122°19'	29.8
5	9	21 Aug.	2116-2150	37°06'	122°50'	5.7
	10	21 Aug.	2236-2314	36°57'	122°59'	10.1
	11	22 Aug.	0032-0115	36°54'	122°38'	24.5
	12	22 Aug.	0152-0231	36°48'	122°30'	23.1
	13	22 Aug.	0302-0341	36°55'	122°25'	10.6
	14	22 Aug.	0412-0450	36°52'	122°17'	24.9
6	15	27 Aug.	2119-2156	34°40'	122°14'	5.8
	16	27 Aug.	2241-2320	34°48'	122°02'	8.0
	17	28 Aug.	0040-0122	34°53'	121°51'	5.9
	18	28 Aug.	0214-0251	35°07'	121°29'	10.1
	19	28 Aug.	0325-0402	35°15'	121°26'	19.6

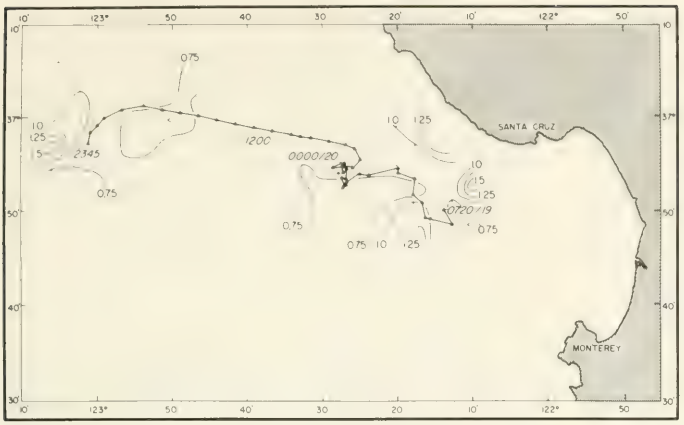

FIGURE 6.—Movements of albacore number 5 as indicated by ultrasonic tracking and the distribution of surface chlorophyll in milligrams per cubic meter.

chlorophyll a, as much as three to four times lower in waters where upwelling had been taking place on 17 August (Figure 6). Also, measurements of ^{14}C uptake indicate that the rate of primary production was about 33% lower, 1,014 mg C/m^2 per day, than it had been when fish number 4 was tracked. In addition, estimates of biomass of potential albacore forage organisms taken in midwater trawl hauls made during tracking operations for fish number 5 were less, ranging from about 6 to 25 ml/1,000 m^3 of water filtered (Table 4), than during tracking operations for fish number 4. (Relatively low chlorophyll a values (Figure 7) and albacore forage biomass values (Table 4) were also observed during tracking operations for fish number 6.)

While tracking information on only two fish does not provide sufficient data from which to make generalizations, the results suggest that 1) albacore concentrate in the vicinity of upwelling fronts, presumably to feed, and 2) albacore move away from the immediate area when upwelling ceases and the upwelling front is no longer present at the surface. Pearcy and Keene (1974) discussed the possibility of albacore congregating in the region of upwelling fronts. The concentration of albacore in the vicinity of upwelling fronts has also been indicated by high catch rates made by fishing and research vessels near upwelling fronts (Pearcy and Mueller 1970; Panshin 1971; Laurs 1973).

Relationship of Albacore Movements to Other Sea Surface Temperature Fronts

During the tracking operations, it appeared that fish numbers 5 and 6 tended to slow down

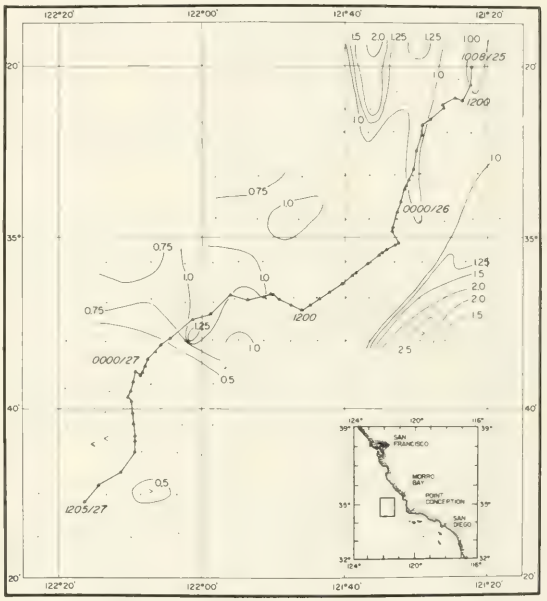

FIGURE 7.—Movements of albacore number 6 as indicated by ultrasonic tracking and the distribution of surface chlorophyll in milligrams per cubic meter.

when crossing temperature fronts where the temperatures on both sides of the front were within the favorable range for albacore. To examine this more closely, mean speeds were estimated for tagged fish when they were within a 5-nmi distance before crossing and after crossing the temperature front and when crossing the front. A sea surface temperature front was defined as a change in surface temperature of 0.5°C or larger in a nautical mile (0.003°C/m). The results are summarized in Table 5 and show that for the three cases examined, 1) the mean speed was slower when crossing the front than it was before

TABLE 5.—Mean speed crossing temperature front[1] and mean speed within 5-nmi radius before and after.

Item	Fish no.	Date	Time	Total (h)	Total distance (nmi)	(km)	Mean speed (knots)	(cm/s)
Before	5	8/19	1330-1600	2.5	5.0	9.3	2.0	103
At front	5	8/19-20	1600-0300	11.0	7.8	14.4	0.7	36
After	5	8/20	0300-0800	5.0	7.0	13.0	1.4	72
Before	6	8/26	1700-1900	2.0	5.6	10.4	2.8	144
At front	6	8/26	1900-2100	2.0	3.7	6.9	1.8	93
After	6	8/26-27	2100-0200	5.0	8.0	14.8	1.6	83
Before	6	8/26	0800-1230	4.5	6.1	11.3	1.4	72
At front	6	8/26	1230-1400	1.5	2.0	3.7	0.7	36
After	6	8/26	1400-1600	2.0	5.2	9.7	2.6	134

[1] $\Delta T \geq 0.5$°C/1.0 nmi.

crossing the front in all three cases, and 2) the mean speed was slower when crossing the front than after crossing the front in two cases. These data should be viewed with caution, however, because in two instances, daytime and nighttime data were used together and some of the differences in speed may be due to variation associated with time of day. The relationship did hold up well in the single case when daytime data only were used.

We think the changes in swimming behavior observed at temperature fronts reflected perception and response to the increased temperature gradient per se. In the case of the alteration in the swimming pattern of fish number 5 as it encountered a temperature front at lat. 36°53'N, long. 122°27'W (Figure 3), there was no sharp gradient in any of the other environmental parameters we measured.

That tunas can perceive abrupt temperature changes as small as 0.1°C has been demonstrated by Steffel et al. (1976) for captive kawakawa, *Euthynnus affinis*. Moreover, a mechanism has recently been suggested (Neill et al. in press) whereby tunas might be able to orient themselves in temperature gradients much gentler than those of our fronts, perhaps even as slight as 0.0001°C/m; this speculative mechanism invokes the large thermal inertia of tunas as a device for thermal "memory."

Movements of Albacore in Relation to Vertical Thermal Structure

The availability of albacore in offshore waters has been shown to be related to vertical thermal structure (Laurs and Lynn[7]). However, no obvious relationship was observed in this study between the movements of sonic-tagged albacore in coastal waters and subsurface temperature structure. This may be due to the complicated vertical temperature structure that was observed in the areas where fish were tracked and the lack of data on the depth of the fish.

SUMMARY

Six albacore were tagged and tracked with ultrasonic equipment for periods ranging from 2 to 50 h and distances ranging from 6.5 to 150.7 km (3.5 to 81.3 nmi). The average swimming speed for these fish tracked between 27.8 and 50.0 h was 1.6 knots (82 cm/s) with each fish exhibiting slightly faster swimming speeds during the day than during the night. The mean swimming speeds observed during the tracking experiment are similar to estimates of swimming speed derived from passive tagging results and about twice the calculated minimum swimming speed necessary to maintain hydrostatic equilibrium.

The tracking experiment indicated that oceanographic conditions may play an important role in the local concentrations and movements of albacore in coastal waters. The movements of fish appeared to be related to the distribution of sea surface temperature, with transmitter-tagged fish spending very little time in water with surface temperatures less than 15.0°C. The results also indicate that upwelling temperature fronts may markedly influence the local concentration of albacore, with albacore tending to concentrate in the vicinity of upwelling fronts, presumably to feed, and moving away from the immediate area when upwelling ceases and the upwelling front is no longer present at the surface. There was also some indication that albacore tended to slow down when crossing sea surface temperature fronts

[7] Laurs, R. M., and R. J. Lynn. 1974. The offshore distribution and availability of albacore during early-season and the migration routes followed by albacore into North American waters. SWFC Admin. Rep. LJ-74-47:19-46.

where the temperatures on both sides of the front were within the optimal range for albacore.

Finally, the tracking experiment demonstrated that acoustic tracking of albacore is feasible and that it can be a useful tool in studies designed to understand better the relationships between albacore and the marine environment.

ACKNOWLEDGMENTS

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ANNUAL FLUCTUATIONS IN BIOMASS OF TAXONOMIC GROUPS OF ZOOPLANKTON IN THE CALIFORNIA CURRENT, 1955-59

J. M. COLEBROOK[1]

ABSTRACT

Year-to-year fluctuations in the abundance of the zooplankton of the California Current region, from 1955 to 1959, have been studied. The abundance of zooplankton was measured in terms of the biomass of each of 17 major taxonomic categories (generally Class or Order). Principal components analysis was used to produce concise descriptions of the major elements of the fluctuations in the abundance of the categories in each of 14 areal subdivisions of the survey area. Considerable coherence with respect to annual changes was found both between the taxonomic categories and between the areas. The principal common element in the fluctuations could be associated with a marked increase in the temperature of the surface waters which occurred in 1957 and persisted through 1958 and 1959. A less pronounced but still quite clear common element in the fluctuations could be associated with year-to-year fluctuations in the amount of coastal upwelling in the area.

Since 1949, the regular surveys conducted by the California Cooperative Oceanic Fisheries Investigation (CalCOFI) program have yielded information about a variety of physical, chemical, and biological parameters (see, e.g., Marine Research Committee 1957). For the CalCOFI survey cruises during January, April, July, and October for each of the years from 1955 to 1959, samples of zooplankton were analyzed to provide estimates of the biomass for each major taxonomic category within the zooplankton (Isaacs et al. 1969).

These data were generously made available to the author by J. D. Isaacs to provide material for a study of year-to-year changes in the abundance of the major components of the zooplankton. As stated by Isaacs et al. (1969), "Selection of the years 1955 through 1959 for analysis of biomass distribution was dictated by interest in the occurrence and nature of patterns of seasonal and annual variability among the functional groups of zooplankton. During this time, yearly mean temperatures above the thermocline shifted upward from the relatively cold years of 1955 and 1956 to the relatively warm years of 1958 and 1959."

The object of the study described in this paper is to describe the annual changes, from 1955 to 1959, in the abundance of the zooplankton of the CalCOFI survey area in as much detail as is available from the survey data in order to discover whether observed changes can be associated with environmental fluctuations.

MATERIAL

The details of the procedures for deriving biomass estimates have been described by Isaacs et al. (1969), who also give the reasons for the selection of the particular set of taxa (listed in Table 1). It was their intention to provide estimates of the "nutrient quality" of the standing crop of zooplankton as well as an index of "trophodynamic complexity." The categories were chosen to represent the quality and quantity of zooplankton as food for fish rather than as indicators of variability of the zooplankton as such.

TABLE 1.—A list of the taxa from CalCOFI cruises for which biomass estimates are available. They are listed in alphabetical order and a code used in Figures 7 and 10 is given.

Taxa	Code	Taxa	Code
Amphipoda	AMPH	Larvacea	LARV
Chaetognatha	CHET	Medusae	MEDS
Cladocera	CLAD	Mysidacea	MYSD
Copepoda	COPD	Ostracoda	OSTR
Crustacea larvae	CRST	Pteropoda	PTER
Ctenophora	CTEN	Radiolaria	RADL
Decapoda	DECP	Siphonophora	SIPH
Euphausiacea	EUPH	Thaliacea	THAL
Heteropoda	HETP		

The collection method for the standard CalCOFI plankton samples has been described in

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detail by, e.g., Ahlstrom (1954) and Fleminger (1964). Very briefly, the net is 1 m in diameter at the mouth and 5 m long, the filtering section having a mesh size of about 0.5 mm. The net is towed obliquely, from a ship traveling at a speed of about 2 knots, from the surface down to a depth of 140 m and then returned to the surface. The volume of water fitered varies from about 400 to 600 m^3.

Charts of the distribution of biomass for each taxon have been given by Isaacs et al. (1969) for the April and October cruises, by Isaacs et al. (1971) for the January cruises, and by Fleminger et al. (1974) for the July cruises. The station data are held on a magnetic tape file at the Southwest Fisheries Center, National Marine Fisheries Service.

DATA PROCESSING METHODS

For the purposes of presenting summaries of CalCOFI data in a compact form and to permit some smoothing of the data by taking average values, P. E. Smith's proposal for subdividing the survey area into 23 zones was used in this study (Figure 1). The extent of the survey and hence the number of stations occupied varied from cruise to cruise. The station patterns for the cruises included in this study are given in Smith (1971), and a summary showing the numbers of samples in each zone is given in Table 2.

The biomass data are available as grams/1,000 m^3 and estimated to two decimal places. The range of estimates is from zero to over 5,000 g, and within each taxon they are heavily positively skewed.

The results presented here were expressed in terms of relative changes in biomass in time and space within each taxonomic category, and extensive averaging was employed. It was decided, therefore, to apply a logarithmic transformation to the original estimates. Averages based on log transformed values are weighted in favor of the more numerous low values as opposed to arithmetic means, the values of which may be determined largely by small numbers of high estimates.

In order to give zero a value on the transformed scale it is normal to add 1 to the observation prior to transformation. In this case, where the biomass has been estimated to two decimal places, a number of options is available, either 1.0, 0.1, or 0.01 can be added prior to transformation. Trials

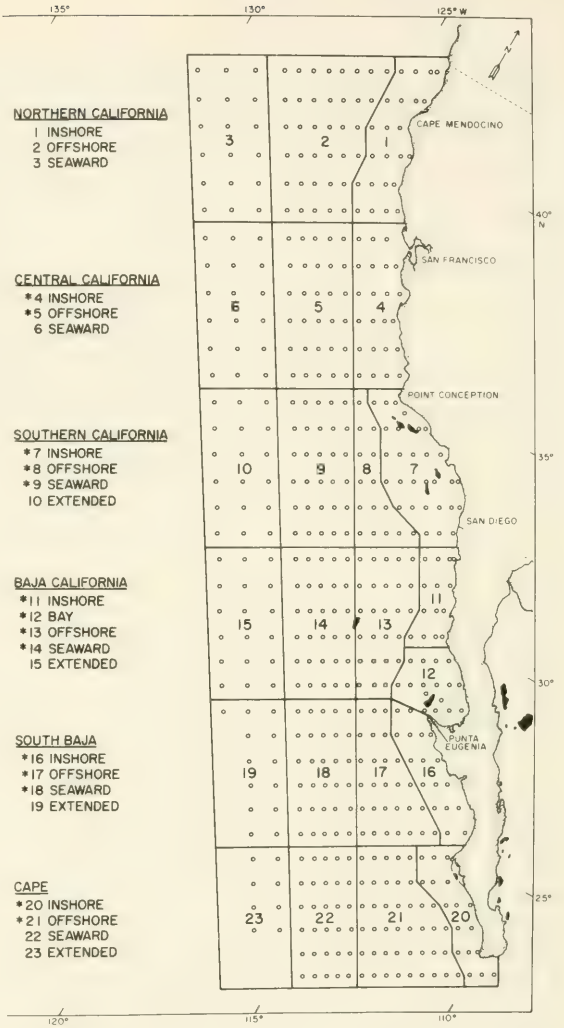


FIGURE 1.—A chart of the area of the CalCOFI survey showing the grid of station positions on which were based the cruises during the period 1955-59. Also shown is the subdivision of the area into the standard zones used in this study. The well-sampled zones for which annual means of biomass were calculated are marked with an asterisk (see Table 2).

involving the calculation of means for each zone for each cruise for a subset of the taxonomic categories indicated that adding 1.0 produced a considerable loss of resolution for means corresponding to less than 1 g/1,000 m^3, and adding 0.01 produced a resolution of low means that appeared to be greater than was warranted by the accuracy of the data. Therefore throughout this study a transformation of the form

$$Y = \log_{10}(10X + 1)$$

TABLE 2.—The numbers of samples collected during each of the January (Jn), April (Ap), July (Jl), and October (Oc) CalCOFI cruises for the years 1955-59 in each of the standard zones (see Figure 1). Annual totals are given in boldface and the grand total is printed in italic.

	1955					1956					1957					1958					1959					
Zone	Jn	Ap	Jl	Oc	To-tal	Jn	Ap	Jl	Oc	To-tal	Jn	Ap	Jl	Oc	To-tal	Jn	Ap	Jl	Oc	To-tal	Jn	Ap	Jl	Oc	To-tal	Grand total
Central California:																										
Inshore	0	0	13	13	**26**	0	18	16	0	**34**	0	0	16	0	**16**	9	21	23	20	**73**	15	20	24	18	**77**	*226*
Offshore	0	0	9	6	**15**	0	9	18	0	**27**	0	0	10	0	**10**	2	21	20	17	**60**	12	14	30	18	**74**	*186*
Southern California:																										
Inshore	20	17	27	22	**86**	21	22	29	27	**99**	0	25	26	26	**77**	18	27	26	29	**100**	29	28	28	27	**112**	*474*
Offshore	4	6	14	6	**30**	4	6	13	9	**32**	0	7	12	6	**25**	5	13	14	9	**41**	6	12	14	9	**41**	*169*
Seaward	3	17	20	6	**46**	5	13	26	6	**55**	0	17	23	17	**57**	11	21	27	17	**76**	11	30	29	17	**87**	*321*
Baja California:																										
Inshore	12	12	13	12	**50**	12	12	14	0	**38**	8	13	12	13	**46**	12	13	11	13	**49**	13	14	13	14	**54**	*237*
Bay	12	13	14	11	**50**	11	12	15	0	**38**	12	15	16	14	**57**	10	16	14	16	**56**	15	16	17	16	**64**	*265*
Offshore	11	13	26	4	**54**	11	11	22	0	**44**	10	20	26	11	**67**	10	25	25	18	**78**	18	26	24	16	**87**	*330*
Seaward	4	12	24	5	**45**	6	16	20	0	**42**	2	16	19	13	**50**	10	30	23	18	**81**	18	29	29	18	**94**	*312*
South Baja:																										
Inshore	16	15	16	14	**61**	13	13	14	0	**40**	16	15	17	17	**65**	15	16	17	17	**65**	17	11	19	17	**64**	*295*
Offshore	8	12	13	6	**39**	8	8	13	0	**29**	8	21	18	12	**59**	12	22	19	20	**73**	19	17	27	20	**83**	*283*
Seaward	3	2	2	3	**10**	1	2	2	0	**5**	1	12	13	13	**39**	3	15	6	7	**31**	8	7	12	8	**35**	*120*
Cape:																										
Inshore	15	0	0	0	**15**	16	16	0	0	**32**	0	19	0	0	**19**	17	0	0	17	**34**	20	10	0	0	**30**	*130*
Offshore	1	0	0	0	**1**	1	10	0	0	**11**	0	22	0	0	**22**	10	0	0	24	**34**	31	14	0	0	**45**	*113*

has been employed. By this transformation, means corresponding to greater than about 0.2 g/1,000 m^3 are virtually on a logarithmic scale while lower means show a progressive transition to an arithmetic scale.

Quarterly means were calculated by averaging the data for the stations in each zone and then these were averaged to give annual values. For those occasions when less than five stations were occupied in any zone, the station data were ignored and a quarterly mean was interpolated by the following method:

1. For each taxonomic category the set of overall zone means (the sum of all the observations for all the cruises in each zone divided by the total number of stations occupied in the zone) was calculated. The set of overall quarterly means (the sum of all the observations for all the cruises in each quarter divided by the number of stations in each quarter) was calculated.
2. For each missing value the sum of the remaining means for the other zones for the cruise and the sum of the corresponding overall zone means were calculated. The latter was weighted by the ratio of the relevant overall quarterly mean to the grand mean and the missing value then calculated as the product of the remaining zone means for the cruise and the weighted sum of the overall zone means.

From these quarterly means, annual means were calculated for each taxon for each of a set of regularly sampled zones (those marked with an asterisk in Figure 1); and principal components analysis was used to extract from these data the main patterns of year-to-year change in biomass. This is a technique of multivariate analysis (see, e.g., Kendall 1957) which generates a sequence of variables known as components with, in this case, values for each year, which are the weighted sums of the standardized data variables, in this case sets of annual means of the taxonomic categories. The sets of weighting factors, with values for each taxonomic category, are the successive latent vectors of the correlation matrix derived from the original data, in this case the table of correlations between the annual variations in abundance of all possible pairs of taxonomic categories. The first latent vector generates a component which has the largest possible variance. The second vector generates a component which has the largest possible variance in relation to the residual following the removal of the variability associated with the first component, and so on. If the original data are coherent to any extent, it is normal for the first few components to account for a large proportion of the variability of the original data array.

GEOGRAPHICAL DISTRIBUTIONS

To provide some geographical background to the study of year-to-year changes in biomass, charts of the overall mean for each taxon in each standard zone were prepared. In order to search

for possible relationships between the geographical distributions of the taxonomic categories, these data were subjected to a principal components analysis.

Figure 2 is a graph of the first latent vector plotted against the second. The graph has a point for each taxonomic category, and the disposition of points represents in a spatial form the relationships between the geographical distributions of the taxonomic categories with respect to the first two components which, in this case, account for 61% of the variability of the original geographical distributions. The interrelationships are probably best regarded in the form of a more or less circular sequence; only the point for Medusae falls well off the sequence.

Figure 3 shows charts of the first two components. The first component shows a very clear north to south, alongshore gradient; and the second shows an equally clear inshore to offshore gradient, indicating that the sequence of categories in Figure 2 runs from categories with northern distributions (Siphonophora to Radiolaria) to inshore distributions (Euphausiacea to Cladocera) to southern and inshore distributions (Larvacea to Mysidacea) to offshore distributions (Heteropoda to Ostracoda). Figure 4 shows the

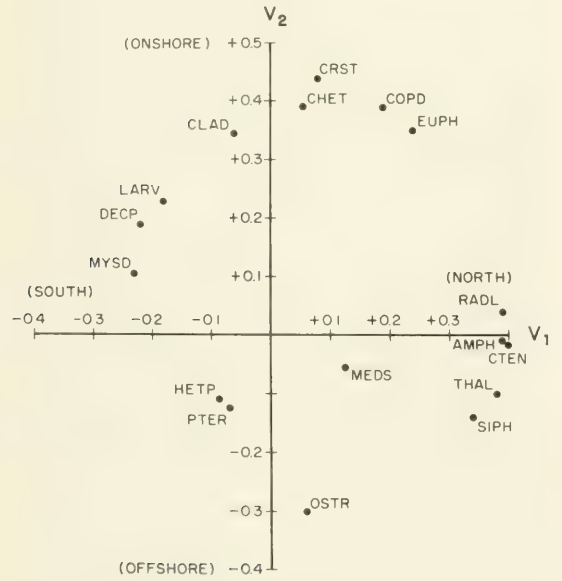


FIGURE 2.—A plot of the first vector against the second vector derived from a principal components analysis of the geographical distributions of the taxa. A key to the abbreviations of the names of the categories is given in Table 1.

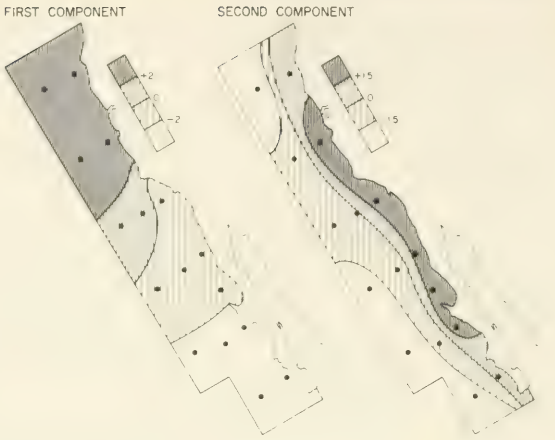


FIGURE 3.—Charts of the first and second components derived from a principal components analysis of the geographical distributions of the taxa.

distributions of the taxonomic categories arranged in this sequence. They are based on averages of the transformed data, for each zone, for each quarterly cruise for the period 1955-59, excluding zones for which fewer than five stations were occupied. These distributions show variability other than that involved in their relationships with the first two components; nevertheless, the north to inshore to south to offshore sequence can be seen fairly clearly. Heteropods and Pteropods are firmly placed in the sequence of taxonomic categories in the vector plot in Figure 2. They have, however, fairly low values compared with the other categories, and only parts of their distributions conform with the south to offshore transition indicated by their position in the vector plot. The distribution of Medusae (Figure 4) can be seen to include areas of relatively high biomass both in the north and in the south, and clearly it does not fit into the sequence of the other categories.

It is obviously unrealistic to attempt to classify the internally diverse taxonomic categories used here in terms of geographical distribution types such as Brinton (1962) found for Euphausiacea. Brinton found that the alongshore axis of the California Current in the CalCOFI survey area was characterized by transitions from "subarctic" species in the north to "transition" species in the region between lat. 30° and 40°N to "equatorial" species in the south. "Central" species occurred offshore and some "boundary" species occurred inshore in the area. McGowan (1971) has shown

that these patterns are reflected generally in the distribution of the plankton of the Pacific Ocean. It may, nevertheless, be significant that the pattern of distribution of the taxonomic categories reflects both the alongshore and the inshore-offshore transitions in the distribution of the Euphausiacea.

YEAR-TO-YEAR FLUCTUATIONS IN BIOMASS

Annual means of biomass were calculated, as described above, for each taxonomic category (Table 1) for each of the well-sampled standard zones (Figure 1) for each of the years 1955-59. Two sets of principal components analyses were carried out, firstly for each of the 14 standard zones on the annual fluctuations in biomass of each taxonomic category and secondly for each taxonomic category on the annual fluctuations in abundance in each of the standard zones. The same data are involved in both sets of analyses.

Graphs of the first principal components for each of the zone analyses are given in Figure 5. Table 3 shows that these components accounted for between just under one-half and about three-quarters of the total variability; it also shows that all but a very few of the categories showed positive relationships with the components. The graphs show considerable similarity between the various zones. These results indicate that a large element of the year-to-year fluctuation in biomass is common to all the zones and to a vast majority of the taxonomic categories. Nearly all the zones show a relatively high biomass (relative to a mean of zero) in 1955 and 1956 and a low biomass in 1958 and 1959. The data for 1957 vary from zone to zone, perhaps tending to be higher in the northern and offshore zones and lower in some of the southern and inshore zones.

A table was prepared of the corresponding vectors with the taxonomic categories arranged, by trial and error, to give the high positive terms at the top, and the low positive and the few negative terms at the bottom of the table. The final ranking of categories and the vector values are given in Table 4. This rank was compared with the rank of taxa based on the relationships between their geographical distributions (Figure 2) starting with the northern distributions, with Siphonophora and Thaliacea, working round the sequence and ignoring Medusae (also left out of Table 4) to finish with Pteropoda and Ostracoda.

TABLE 3.—For each zone (*a*) the percentage of the total variability of the original data accounted for by the first component and (*b*) the number of taxa with positive first vector values (maximum = 17). The code names for the zones used in Table 4 and Figures 6 and 9 are also given.

Zone	Code	*a*	*b*
Central California:			
Inshore	CCALIN	74	17
Offshore	CCALOF	71	17
Southern California:			
Inshore	SCALIN	63	14
Offshore	SCALOF	58	17
Seaward	SCALSW	58	15
Baja California:			
Inshore	BCALIN	70	15
Bay	BCALBY	66	16
Offshore	BCALOF	52	14
Seaward	BCALSW	48	13
South Baja:			
Inshore	SBAJIN	64	16
Offshore	SBAJOF	56	16
Seaward	SBAJSW	45	12
Cape:			
Inshore	CAPEIN	54	15
Offshore	CAPEOF	53	16

TABLE 4.—The first vectors of principal component analyses for each standard zone with the taxonomic categories ranked as described in the text. Also the rank of the categories derived from Figure 2.

Taxa	CCALIN	CCALOF	SCALIN	SCALOF	SCALSW	BCALIN	BCALBY	BCALOF	BCALSW	SBAJIN	SBAJOF	SBAJSW	CAPEIN	CAPEOF	Atlas rank
Copepoda	0.28	0.28	0.30	0.31	0.36	0.29	0.29	0.30	0.34	0.30	0.30	0.31	0.27	0.30	7
Thaliacea	0.27	0.27	0.30	0.28	0.31	0.28	0.29	0.32	0.33	0.29	0.31	0 29	0.30	0.31	2
Amphipoda	0.27	0.28	0.30	0.32	0.31	0.27	0.28	0.31	0.33	0.28	0.28	0.22	0.29	0.28	4
Siphonophora	0.27	0 28	0.22	0.29	0.23	0.29	0.29	0.25	0.29	0.28	0.30	0.32	0.28	0.28	1
Radiolaria	0.28	0.27	0.30	0.29	0.31	0.28	0.28	0.30	0 28	0.23	0.28	0.20	−.02	0.00	5
Ctenophora	0.26	0.27	0.30	0.26	0.28	0.26	0.26	0.26	0.33	0.27	0.26	0.06	0.16	0.05	3
Decapoda	0.25	0.25	0.26	0.29	0.29	0.27	0.24	0.31	0.29	0.24	0.28	0.29	0.30	0.33	12
Euphausiacea	0.27	0.26	0.28	0.26	0.26	0.28	0.21	0.14	0.17	0.24	0.28	0.18	0.18	0.31	6
Chaetognatha	0.28	0.27	0.30	0.28	0.28	0.27	0.24	0.11	0.27	0.24	0.25	−.26	0.31	0.32	9
Crustacea larvae	0.25	0.06	0.30	0.27	0.22	0.25	0.24	0.17	−.09	0.25	0.31	−.25	0.29	0.11	8
Heteropoda	0.15	0.24	0.14	0.18	0.23	0.16	0.29	0.20	0.07	0.19	0.29	0.19	0.27	0.28	14
Larvacea	0.28	0.27	0.17	0.13	0.24	0.27	0.29	0.21	−.05	0.22	−.08	0.29	0.22	0.23	11
Ostracoda	0.22	0.26	−.01	0.26	0.23	0.12	0.18	0.23	0.13	0.18	0.11	−.21	0.21	0.24	16
Cladocera	0.12	0.19	−.03	0.01	0.03	−.23	0.03	−.25	0.06	0.23	0.17	0.11	0.09	−.08	10
Pteropoda	0.19	0.13	0.10	0.08	−.02	0.04	0.12	−.02	−.19	−.06	0.05	−.08	−.17	0.21	15
Mysidacea	0.15	0.17	−.28	0.09	−.15	0.08	0.11	−.12	−.27	0.26	0.14	−.33	0.29	0.16	13

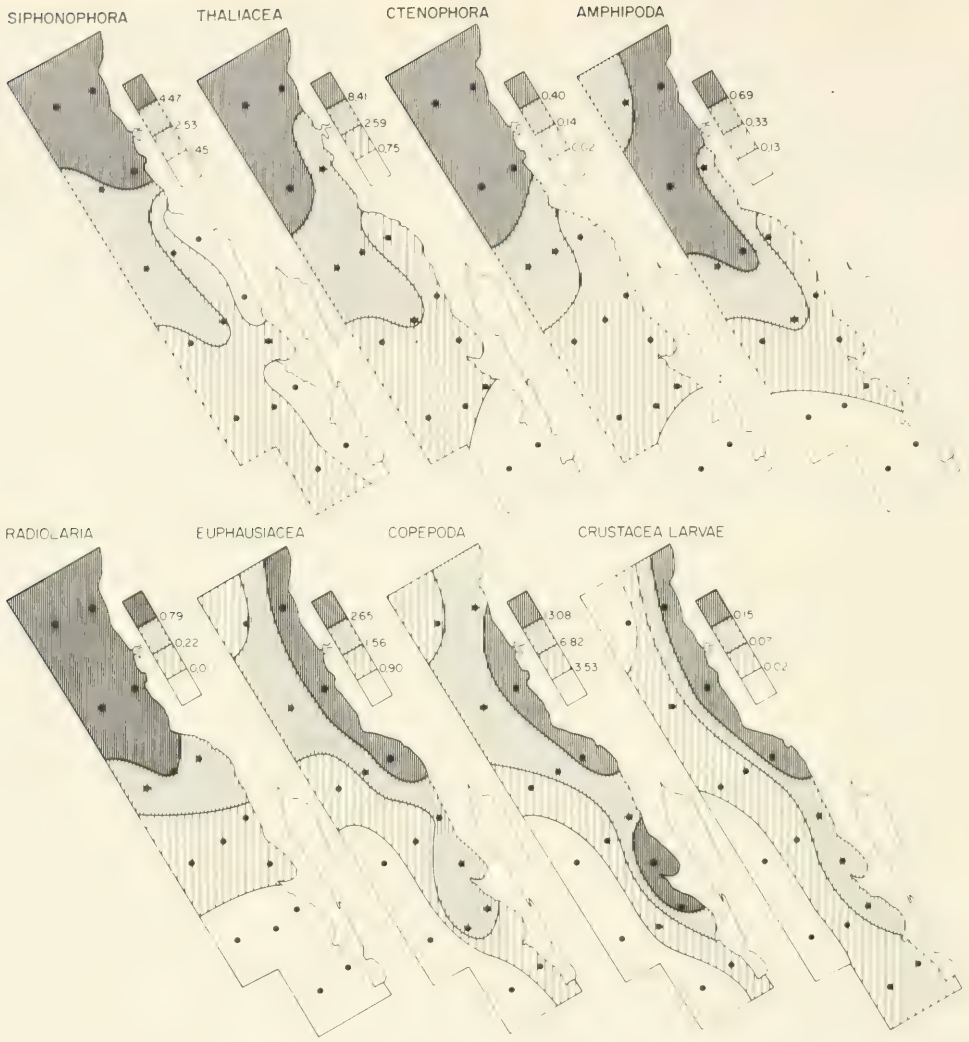


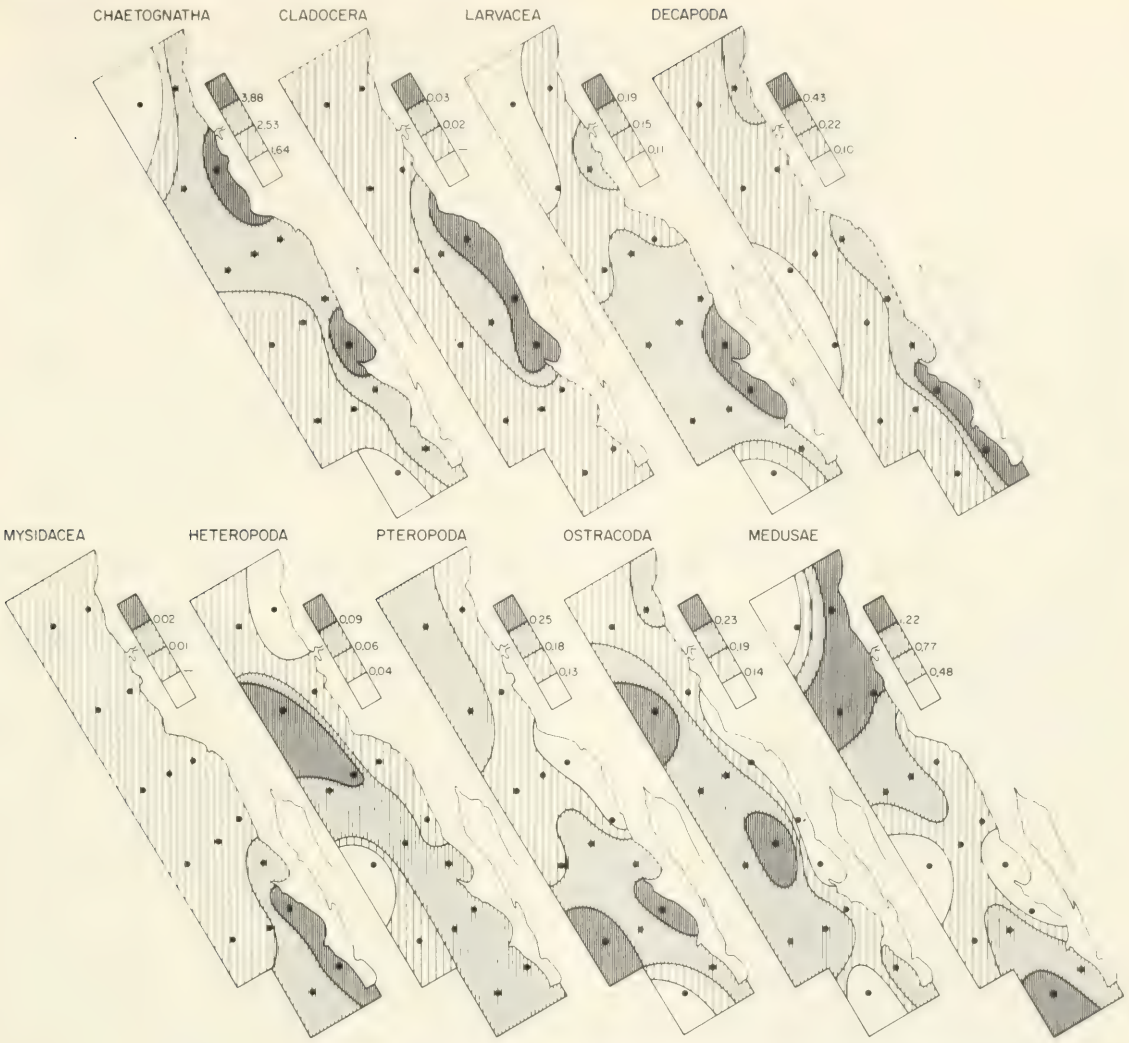
FIGURE 4.—Charts of the geographical distribution of biomass for each of the taxa based on logarithmic means for each standard zone (see Figure 1) for all the CalCOFI cruises for 1955-59. Contours are drawn at levels correspond-

The ranks are given in Table 4, and the value of Spearman's rank correlation coefficient between the two ranks is +0.806 which is significant at the 0.1% level.

Figure 6 shows graphs of the first principal components of the analyses for each taxonomic category with the categories ranked in the same order as in Table 4. All the northern and inshore categories, down to Crustacea larvae in Figure 2, show the same form of year-to-year fluctuations in biomass as do the zones, with relatively high biomass in 1955 and 1956 and low biomass in 1958 and 1959. The remaining categories show some features of this pattern with only Cladocera showing a negative relationship.

These results suggest that whatever influence or influences are responsible for the fluctuations in the plankton either have their origin in the north of the survey area or have a greater effect on those categories with northern patterns of distribution. It is, at least, fairly safe to infer that there is some commonality between the influences which determine geographical distribution and those which are responsible for the form of the year-to-year changes in biomass.

The years from 1955 to 1959 were deliberately



ing to the mean + 1 SD, the mean, and the mean − 1 SD. The keys to the contour levels for each category give the arithmetic values, as grams per 1,000 m^3, corresponding to these levels.

chosen for the production of biomass data to cover a period of marked change in physical conditions and in the distribution of many species in the CalCOFI area. The main features of these changes have been described in the proceedings of a special symposium (Sette and Isaacs 1960). The most striking feature was a considerable warming of the surface waters which started in the south in 1956 and spread through the area during 1957 (see, e.g., Longhurst 1967).

The general form of the change can be typified by the variation in temperature in the top 50 m in the southern California offshore area shown in Figure 7. Favorite and McLain (1973) showed that this is part of a widespread change in surface temperature affecting almost the whole of the North Pacific Ocean. The reasons for the change are not yet completely clear. The initial warming in 1957 appears to be associated with a reduction in the flow of the California Current which occurred between the late summer of 1957 and midsummer 1958. As an index of the flow of the California Current, Saur (1972) used the difference in sea level between Honolulu and San Francisco. A plot of monthly means (with a linear trend removed and adjusted to normal atmo-

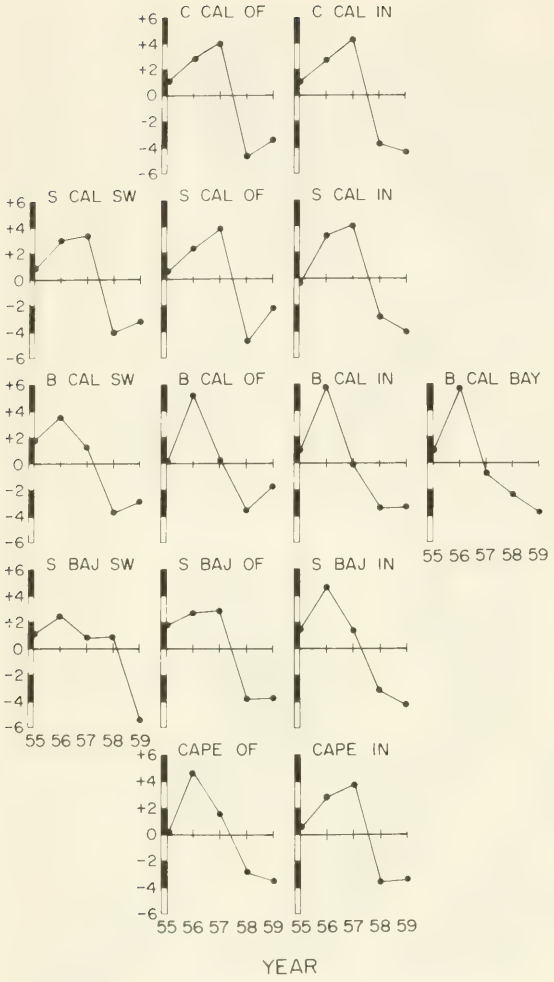


FIGURE 5.—Graphs for each of the well-sampled CalCOFI zones (see Figure 1) of the first principal component of the year-to-year fluctuations in biomass of all the 17 taxa. Each graph is drawn with a mean of zero and the vertical scale is in SD units.

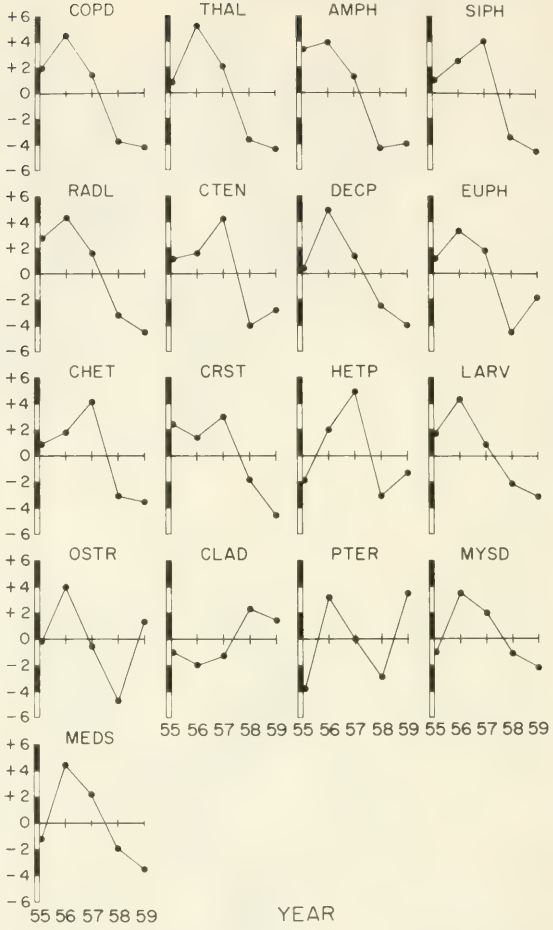


FIGURE 6.—Graphs for each taxon of the first principal component of the year-to-year fluctuations in biomass for all the well-sampled CalCOFI standard zones. A key to the abbreviations of the names of the taxa is given in Table 1. They are in the same order as in Table 4 (see text). Each graph has a mean of zero and the vertical scale is in SD units.

spheric pressure) for 1955-59 is shown in Figure 7. Differences greater than 58 cm are believed to indicate a stronger than normal flow and differences less than 58 cm a less than normal flow. It can be seen that the period of less than normal flow in 1957-58 corresponds well with the timing of the increase in temperature in the southern California offshore zone. In the California Current region, and indeed over most of the eastern North Pacific, the increase in temperature persisted through 1958 and 1959 while the sea level differences indicate a normal or above average flow during this time. The period of below normal flow corresponds with El Niño off the coast of Peru and perhaps with an anomalous weakening of the trade winds of the southern hemisphere and a concurrent reduction of equatorial upwelling (Bjerknes 1966; Favorite and McLain 1973).

Wickett (1967) found a relationship between the year-to-year changes in zooplankton volume for the CalCOFI survey (Thrailkill 1963) and the mean meridional Ekman transport (Fofonoff 1962) for January to August in the previous year at lat. 50°N, long. 140°W (over 1,000 miles upstream from the CalCOFI survey area) for the years 1952-59. He suggested that a major cause of variation in the abundance of zooplankton in the California Current region is the change in the

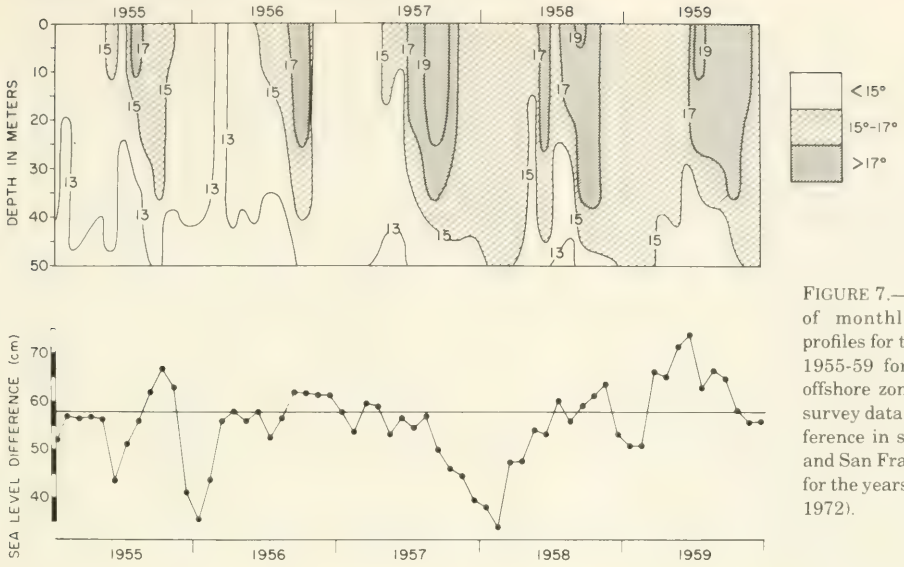


FIGURE 7.—Top) A contoured diagram of monthly vertical temperature profiles for the upper 50 m for the years 1955-59 for the southern California offshore zone (see Figure 1). CalCOFI survey data. Bottom) A graph of the difference in sea level between Honolulu and San Francisco at monthly intervals for the years 1955-59 (plotted from Saur 1972).

proportion of the superficial wind-driven water that is swept southward out of the North Pacific subarctic circulation.

There seems little doubt that the change in temperature in 1957 and its persistence through 1958 and 1959 is related to the relative reduction in biomass of the zooplankton associated with the first principal components of all zones and most of the taxonomic categories. The data presented by Wickett showed a marked reduction in southward transport at lat. 50°N, long. 140°W during 1958 and 1959 and this, coupled with the reduction in the flow of the California Current in 1957 and 1958 (Figure 7), would appear to support Wickett's suggestion of a direct influence by water movements. The relationship between the north to south geographical gradient (Figure 3) and the first principal components is also entirely consistent with this hypothesis.

An examination of the remaining components for each of the zones indicated the existence of a second pattern of fluctuation common to most of the zones. In Figure 8 are given graphs of a component, other than the first, for each zone selected to give the best approximation to a form common to all the zones. In 8 of the 14 zones it is the second component; in the remaining zones it is either the third or the fourth component. Given the quantity and the quality of the original data and considering the large proportion of the variability of the data associated with the first components, the lack of consistency in the position of the common pattern among the components is perhaps not surprising. Figure 9 shows the same for each taxonomic category; again the majority are second components and only one, for Radiolaria, is the fourth component. The main features of the pattern are a low in 1957 and highs in 1956 and 1958; 1955 and 1959 tend to be low but their positions vary somewhat within both the zones and the taxonomic categories.

Coastal upwelling is a feature of the California Current region, and Bakun (1973) has produced estimates of relative fluctuations in upwelling at a number of positions along the west coast of North America. They are based on estimates of the offshore component of the Ekman transport which is in turn estimated from atmospheric pressure fields.

Monthly means of the upwelling index for five positions off the coast at latitude and longitude 36°N, 122°W; 33°N, 119°W; 30°N, 116°W; 27°N, 116°W; and 24°N, 113°W, for the period 1955-58 were extracted from Bakun's report. Uncertainties about the differences in absolute terms between the estimates at different positions particularly off southern California, discussed by Bakun, suggested that principal components might provide a good method of summarizing the data from this set of positions. For each calendar month, analyses were carried out on the index estimates for the five positions and the 5 yr. Examination of the components showed that a pattern common to the first 7 mo of the year was

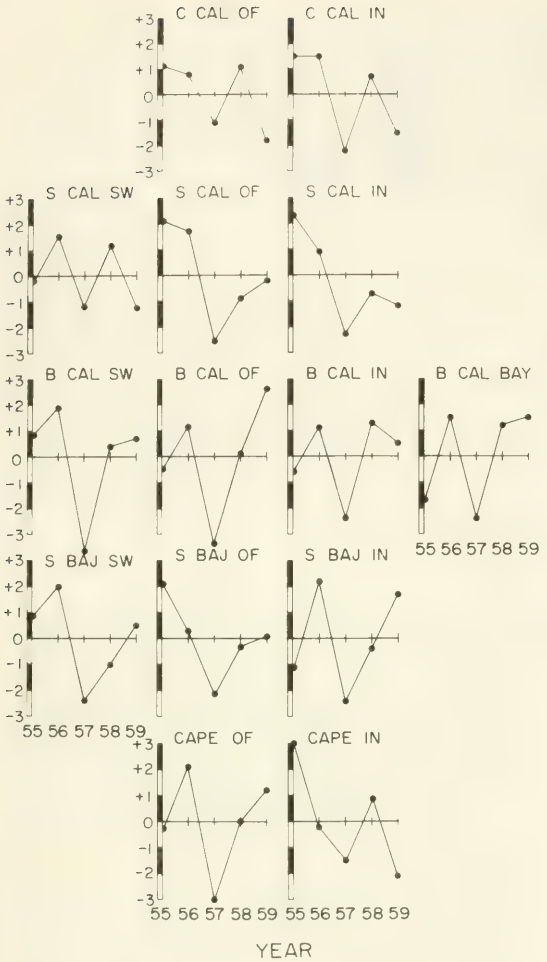


FIGURE 8.—Graphs, for each CalCOFI standard zone, of principal components of annual fluctuations in biomass. See text for the method of selection of the components, see also the legend to Figure 6.

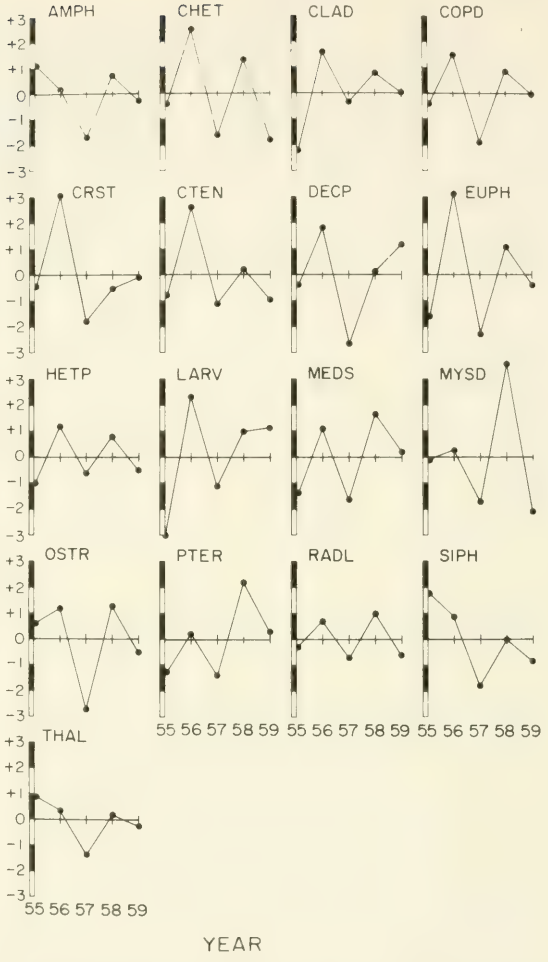


FIGURE 9.—Graphs, for each taxonomic group (Table 1), of principal components of annual fluctuations in biomass. See text for the method of selection of the components, see also the legend to Figure 7.

present within the components, and graphs of these are given in Figure 10. The pattern was found as the first component in all the months except March and April where it was found in the second component. Graphs of the first components for August to December are also given in Figure 10.

There is a marked similarity between the pattern of year-to-year fluctuations in upwelling as represented by the components for the first 7 mo of each year and the fluctuations in biomass of the zooplankton represented by the components shown in Figures 8 and 9, and it is reasonable to assume that some form of causal relationship is involved. As with the first component in relation to the temperature range, the precise mechanisms involved cannot be inferred from the information here. Upwelling has effects on the vertical temperature structure and particularly on the timing of the establishment of a clear thermocline. It can also be expected to have a considerable influence on the supply of nutrients. It is probable, therefore, that the effect on the zooplankton is an indirect one through the influence of vertical stability of the water column and the supply of nutrients on primary production processes. Peterson (1973) has established a relationship between year-to-year variation in upwelling

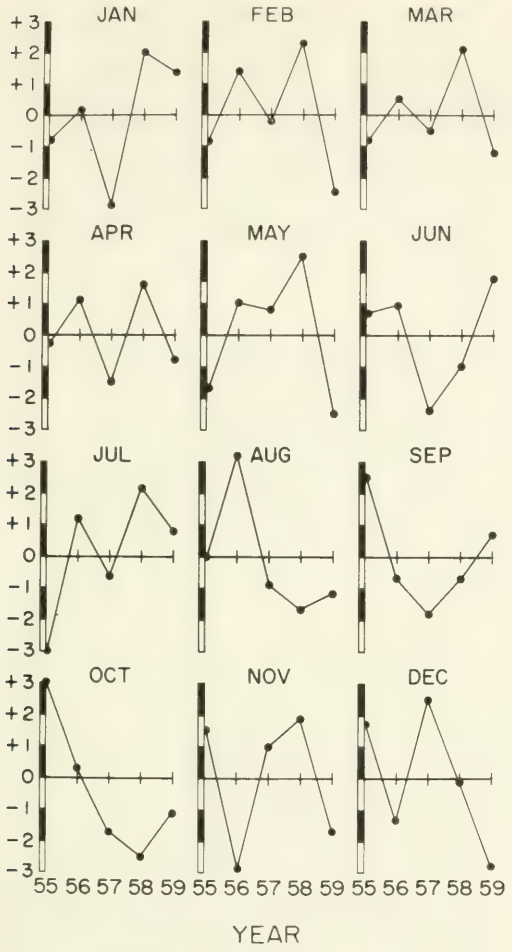


FIGURE 10.—Graphs of principal components of upwelling index for the CalCOFI survey area for each month for the years 1955-59. See text and Bakun (1973).

off the coast of Oregon and the catch of the Dungeness crab, *Cancer magister*, with a time lag of about 18 mo. He attributed this to an increased food supply in years with pronounced upwelling, implying a relationship between upwelling and plankton similar in sign to that found further south in the California Current.

CONCLUSIONS

At least during the period 1955-59, a considerable proportion of the variability from year to year in the biomass of zooplankton, as represented by estimates for the taxa listed in Table 1, can be associated with hydrographic events, variations in the strength of the California Current, and variations in the intensity of coastal upwelling. The precise mechanisms involved are not clear, but in relation to the California Current there is a similarity in the relationships within the taxa with respect to both geographical distribution and annual fluctuations in abundance which suggests that advection of stocks may be involved to a considerable extent. The influence of upwelling on primary production through effects on temperature stratification and the supply of nutrients probably accounts for the relationship with the zooplankton.

The only data that have been produced routinely from the whole series of CalCOFI cruises, which relate to plankton other than fish eggs and larvae, are in the form of displacement volumes of unsorted samples (Smith 1971). The marked coherence between the various taxonomic categories suggests that these data can be expected to produce estimates of long-term variations which indicate real changes in the abundance of the zooplankton. Such data cannot, however, reflect the geographical differentiation within the zooplankton, and this imposes a limit, to the extent to which they can be used, to provide the basis for the examination of the influences of a complex of environmental factors of the kind suggested by this study as playing an important role in determining the year-to-year fluctuations in the plankton.

The taxonomic categories used in this study were selected by Isaacs et al. (1969) to represent the plankton as food for fish. I have used them to represent fluctuations in the zooplankton as such for the 1955-59 period.

For future studies the only definitive method of selecting taxa to represent year-to-year changes in the zooplankton is by trial and error: there are, moreover, numerous possibilities, and the labor involved would be prohibitive if some compromise is not made. It is indicated above that there is a tendency for taxa which have similar geographical distributions also to show similar year-to-year fluctuations in abundance. As a first approximation, this fact might be used as a guide to the selection of representative categories. It is implicit that each selected category should be geographically homogeneous, and the set of categories should cover the full range of geographical distributions.

It is probable that the species is the highest taxon for which geographical homogeneity can be assumed, and even here there may be some species which have geographically differentiated races. Isaacs et al. (1969) gave an estimate of about 550

species found, or likely to be found, in the zooplankton of the CalCOFI survey area. Allowing for the fact that somewhere between one-half and three-quarters of these species will probably occur infrequently in samples, the labor involved in routinely analyzing for this number of species is very considerable. The geographical distributions of species belonging to many of the major taxa within the zooplankton have been studied and published in the CalCOFI Atlas series which could provide the basis for the selection of a limited number of species which will represent the range of geographical distributions in the survey area and, hopefully, will provide a good representation of the range of year-to-year fluctuations in abundance.

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My thanks are due to Brian Rothschild, Director, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, for making available to me the facilities of the La Jolla Laboratory. I also thank J. D. Isaacs for furnishing unpublished data. Nancy Wiley and Dorothy Roll were of great assistance in the computations involved in the study and John G. Wyllie helped with some data problems. Finally I must thank Paul E. Smith whose knowledge of the California Current region and of the CalCOFI survey was invaluable. My visit to the La Jolla Laboratory was supported by the U.K. Natural Environment Research Council.

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POPULATION BIOLOGY OF PACIFIC OCEAN PERCH, *SEBASTES ALUTUS*, STOCKS IN THE WASHINGTON-QUEEN CHARLOTTE SOUND REGION, AND THEIR RESPONSE TO FISHING[1]

DONALD R. GUNDERSON[2]

ABSTRACT

Production and catch per unit effort of Pacific ocean perch, *Sebastes alutus*, stocks in the Washington-Queen Charlotte Sound region have declined drastically in recent years, largely as a result of Soviet and Japanese exploitation during 1966-69. In the region off Washington and southern Vancouver Island, production declined from 39,000 metric tons in 1967 to 6,000 metric tons in 1969, and catch per hour declined 45% during the same period. Pacific ocean perch are ovoviviparous, and so their populations lack the resilience of highly fecund, oviparous groups such as the gadoids. Their ability to maintain even current levels of abundance is uncertain.

Age composition, growth rates, and mortality rates were estimated for two separate stocks occupying this region: one in Queen Charlotte Sound, B.C., and one occupying the area off northern Washington and southern Vancouver Island. Instantaneous rate of natural mortality was estimated to lie between 0.1 and 0.2. Recruitment to the fishing grounds is not complete until age 16 and the proportion of each age group vulnerable to fishing was estimated by stock for age groups 10 (0.31-0.35) through 15 (0.87-0.94).

Age at sexual maturity ($t_{0.50}$) differed between stocks, ranging from 9 to 11 yr for females and 6 to 7 yr for males. Fecundity was determined for several females, and the fecundity-length and fecundity-age relationships discussed. For a variety of reasons, all fecundity estimates were regarded as tentative, bearing a rather uncertain relationship to the number of larvae released.

The effects of fishing on stocks of Pacific ocean perch were examined through an approach similar to the yield per recruit analysis that is commonly used in stock assessment, although the computer program developed for this study enabled estimation of exploitable biomass and population fecundity as well as yield per recruit.

Compensatory mechanisms that would tend to restore population fecundity and recruitment to preexploitation levels were discussed, and the limits of some of these mechanisms (density dependent growth and earlier sexual maturation) were explored with the computer program mentioned previously. The results of this analysis suggested that past levels of exploitation went far beyond those levels that could be sustained by Pacific ocean perch stocks on a long-term basis. It was concluded that future rates of exploitation should be regulated so that the annual catch never exceeds 10% of the mean stock biomass on hand during the year.

Pacific ocean perch, *Sebastes alutus* (Gilbert), are found throughout the northern Pacific, from California to the Bering Sea, and as far southwest as the Kurile Islands. Murphy (1968) has shown that species with several reproductive age-groups are well adapted to unpredictable levels of larval mortality, and Pacific ocean perch seem to be a prime example of this line of evolution. Twenty-year-olds are common in this species, and there are 10 or more reproductive age-groups of significance. In the unexploited state, large standing stocks of *S. alutus* accumulated, furnishing a substantial hedge against uncertain larval survival. Quast (1972) estimated the original catchable biomass of *S. alutus* off western North America to be roughly 1,750,000 metric tons.

Commercial fishing for *S. alutus* was initiated in 1946 by U.S. trawlers operating off central Oregon (Alverson and Westrheim 1961). Development proceeded slowly, but by 1955, United States and Canadian vessels were harvesting *S. alutus* from as far north as Queen Charlotte Sound, B.C. Westrheim et al. (1972) have characterized the North American trawl fishery for Pacific ocean perch as undergoing a short development period (1946-51) with low production, a longer period (1953-60) of moderate production, and a short period (1961-66) of increasing production. Since

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1966, Pacific ocean perch production has fallen drastically in several areas fished by these North American trawlers, largely because of excessive catches by Japanese and Soviet fleets.

Japanese and Soviet trawl fisheries for Pacific ocean perch began in the Bering Sea about 1960 and expanded southward into the eastern Gulf of Alaska in 1963. The Soviet fleet operated throughout the Queen Charlotte Sound-Oregon region by 1965, and they were joined by Japanese trawlers in 1966. Catches from the Oregon-Queen Charlotte Sound region were quite high initially (Figures 1 through 3), but the stocks were far too limited to sustain these harvests. By 1969, *S. alutus* stocks were severely depleted throughout the Oregon-Vancouver Island region (Figures 1, 2). Production in the International North Pacific Fisheries Commission (INPFC) Vancouver and Columbia areas plummeted from 39,000 metric tons in 1967 to 6,000 metric tons in 1969 (an 85% decline), and catch per hour by North American trawlers declined 45% during the same period (Westrheim et al. 1972). Data on catch per unit effort (CPUE) suggest that the exploitable biomass of Pacific ocean perch in the Vancouver-Columbia region has changed little since 1969, despite the fact that a series of relatively strong year classes have recruited to the fishery.

Pacific ocean perch stocks in Queen Charlotte Sound were affected less drastically by fishing than those in the Oregon-Vancouver Island region. Biomass estimates and CPUE data (Westrheim et al. 1972) indicated that *S. alutus* were initially more abundant in the former area and that they did not undergo such intensive exploitation. During 1966-68, production declined 50% while CPUE of Washington trawlers declined 36%. Fishing effort was reduced substantially after March 1971, when most of Queen Charlotte Sound was declared to be an exclusive Canadian fishing zone. Bilateral agreements between Canada and the United States allowed the traditional United States fishery for *S. alutus* to continue, but Japanese and Soviet fishing was prohibited. Recent information, however, indicates that in 1974, large catches of Queen Charlotte Sound Pacific ocean perch were made by Japanese vessels

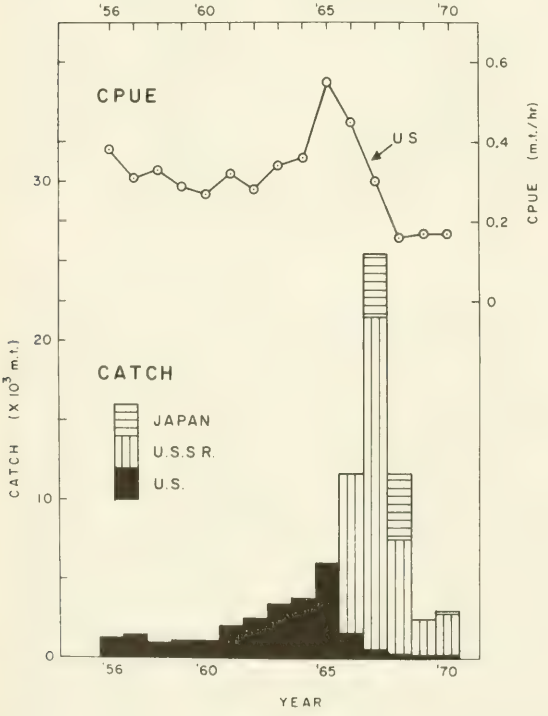

FIGURE 1.—Catch and CPUE data for Pacific ocean perch in the INPFC Columbia area (from Westrheim et al. 1972).

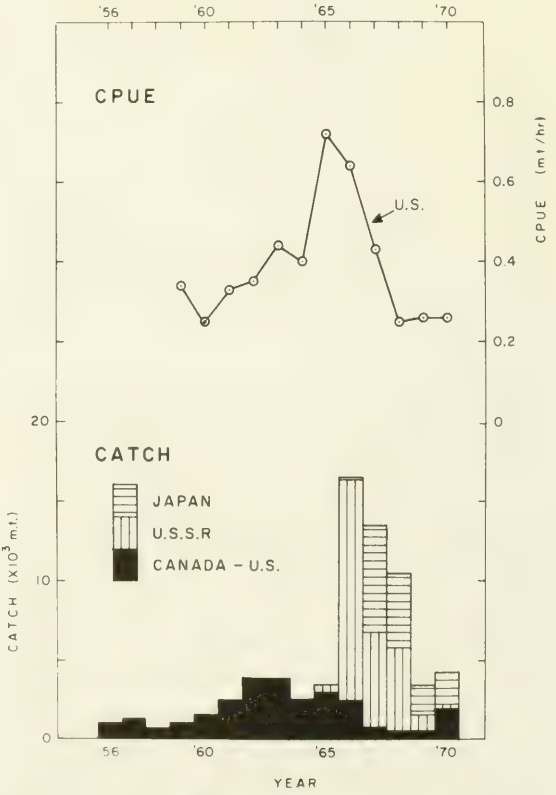

FIGURE 2.—Catch and CPUE data for Pacific ocean perch in the INPFC Vancouver Area (from Westrheim et al. 1972).

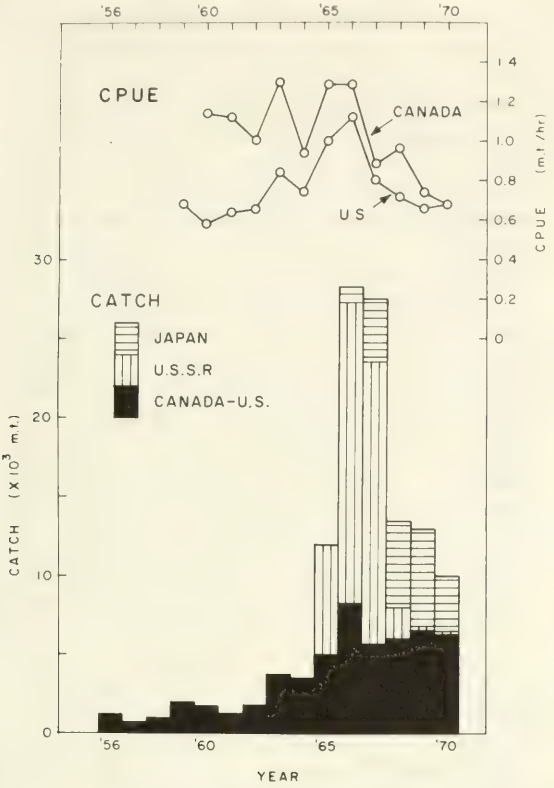

FIGURE 3.—Catch and CPUE data for Pacific ocean perch in Queen Charlotte Sound (from Westrheim et al. 1972).

operating outside the Canadian fishing zone (Gunderson et al. 1977).

Both biomass and longevity have been drastically reduced for Pacific ocean perch throughout the Washington-Queen Charlotte Sound region, and it seems unlikely that the current situation will be stable over the long term. The purpose of this study is to outline the population biology of *S. alutus* stocks in the Washington-Queen Charlotte Sound area and to examine their immediate and long-term response to different harvesting strategies.

METHODS AND MATERIALS

Delineation of Stocks

Two stocks of *S. alutus* will be examined and contrasted: one in Queen Charlotte Sound (QCS) and one inhabiting the waters off northern Washington and southern Vancouver Island (WVI).

The QCS stock is contained wholly within Queen Charlotte Sound. North of lat. 52°N, the continental shelf off western Graham Island is quite narrow and there is little available habitat for *S. alutus*. Recent work by Westrheim[3] has shown that previously unexploited stocks exist in Moresby Gully, an undersea canyon extending into Hecate Strait, north of lat. 52°N. The Triangle Islands form a definite southern limit for this stock, since Pacific ocean perch catches immediately south of these islands are almost negligible. Pacific Marine Fisheries Commission (PMFC) statistical areas 5A and 5B offer a convenient unit for studying this stock.

The northern limit of the WVI stock lies somewhere near the middle of Vancouver Island and, for practical reasons, this was represented by the northern boundary of PMFC area 3C (lat. 49°N). Pacific ocean perch catches in PMFC area 3D have been quite limited historically (Figure 4), and during 1966-72, only 13% of the Washington landings in the INPFC Vancouver area came from there (Table 1).

The southern limit of the WVI stock is more difficult to establish. Since Pacific ocean perch catches by Washington trawlers fall off sharply south of PMFC area 3B-3C (lat. 47°20′N), this was the boundary used throughout this study. This boundary, as well as the others used in this report, is in basic agreement with Snytko (1971), whose

[3]Westrheim, S. J. 1974 Echo-sounder and trawl survey of Queen Charlotte Sound and southern Hecate Strait, 1971-73. Fish. Res. Board Can. Manuscr. Rep. 1307, 43 p.

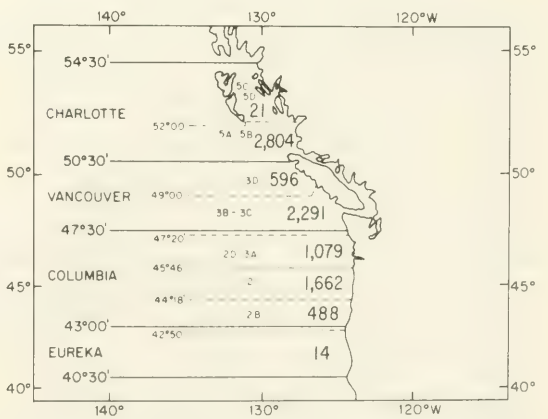

FIGURE 4.—Chart of the northeastern Pacific Ocean showing INPFC and PMFC statistical areas used in this study. Mean annual Pacific ocean perch catch (metric tons) during 1960-65 (heavy lettering) is shown for each PMFC Area.

TABLE 1.—Catches (in metric tons) of Pacific ocean perch by different components of the international trawl fleet, 1966-72.

	Washington			United States and Canada		All nations	
Year	3B-3C	3B-3D	5A-5B	3B-3D	5A-5B	3B-3D	5A-5B
1966	2,104	2,283	5,616	2,358	8,252	16,358	27,054
1967	701	783	5,341	805	5,745	17,746	26,741
1968	459	526	4,787	552	6,051	9,905	13,492
1969	462	573	4,992	583	6,628	4,513	12,951
1970	980	1,208	4,308	1,955	6,077	4,955	9,854
1971	638	718	2,925	1,155	4,165	4,138	4,867
1972	419	504	3,364	624	5,561	3,082	7,842
Total	5,763	6,595	31,333	8,032	42,479	60,697	102,801

research cruise data suggested that the two most significant aggregations of *S. alutus* in the Vancouver-Oregon region were found at lat. 48°-50°N and lat. 46°-47°N. For all practical purposes then, PMFC Statistical areas 3B and 3C offer a convenient unit for studying the WVI stock.

Data Employed

Production records used in this study came from the Washington State Department of Fisheries, PMFC, INPFC, and from data furnished during U.S.-U.S.S.R. scientific meetings.

Landings by Washington trawlers made up a relatively small proportion of the total international landings during the 1966-72 study period, but the quality of their production records is such that the CPUE data from this fleet offer the best available index of stock abundance. During 1966-72, the Washington landings made up 30% of the total international catch from Queen Charlotte Sound, and 11% of the catch from the INPFC Vancouver area (Table 1). Washington trawlers accounted for the bulk of the North American landings in these areas, however, landing 74% of the Pacific ocean perch caught in Queen Charlotte Sound and 82% of those from the INPFC Vancouver area during 1966-72.

Most of the data on age composition (as determined from otoliths), length composition, and maturity were obtained by sampling the catches landed by Washington trawlers and were collected during 1967-72. Data from research vessel cruises off Washington and Oregon were used to estimate growth rates and fecundity-length relationships for the WVI stock.

MIGRATIONS AND AVAILABILITY

General Features of the Life History

Extensive investigations into the life history of *S. alutus* have been carried out in the Bering Sea (Paraketsov 1963; Pautov 1972; Chikuni 1975), Gulf of Alaska (Lyubimova 1963, 1964, 1965; Fadeev 1968; Chikuni 1975), and in the Queen Charlotte Sound-Oregon region (Alverson and Westrheim 1961; Westrheim 1970, 1973, 1975; Gunderson 1971, 1974; Snytko 1971). These studies have shown that there are several basic similarities in the life history and biology of Pacific ocean perch throughout its range.

Age and growth analyses have shown that *S. alutus* attain sexual maturity relatively late in life (6-10 yr), grow slowly, and are long-lived. In lightly fished stocks, *S. alutus* may reach an age of 30 yr (Alverson and Westrheim 1961; Paraketsov 1963).

Sebastes alutus is an ovoviviparous species, with three distinct phases in its reproductive cycle. These are: mating (when spermatozoa are transferred from males to females), fertilization (when the ova are actually fertilized), and spawning (when the larvae are released).

Well-defined bathymetric migrations occur in all areas. Pacific ocean perch occupy relatively shallow water during the summer feeding period, then move to deep water during winter. The depths inhabited seem to vary little throughout the geographic range, despite significant differences in thermal conditions (Table 2). Mating occurs shortly before or during migration from shallow water, but fertilization and embryo release do not occur until the fish are in deep water.

The larvae of *S. alutus* are pelagic and do not settle into a demersal existence until 2-3 yr old. Juveniles and young adults are confined to the shallowest portions of the adult bathymetric range, so that size and age composition vary widely at different depths.

Despite these common characteristics, there are substantial geographic differences in life history and migration patterns, even within the relatively restricted region dealt with in this study. For this reason, migration patterns, seasonal availability, age composition, growth, age at maturity, and

TABLE 2.—Depth and temperature characteristics of Pacific ocean perch habitat.

	Depths of maximum abundance (m)		Temperature (°C)	
Area	Summer	Winter	Range	Optimum
Vancouver-Oregon (Snytko 1971)	200-300	350-450	4.0-9.5	6-8
Gulf of Alaska (Lyubimova 1965)	180-250	250-420	2.5-6.5	3-5
Bering Sea (Pautov 1972)	150-350	350-450	1.0-6.0	3-4

fecundity must be discussed separately for the QCS and WVI stocks.

Migrations and Availability Within the Study Area

Availability of *S. alutus* fluctuates widely over short periods of time. Short-term fluctuations in availability were quite evident during a series of 2- to 3-wk research cruises off the Washington coast (Gunderson 1974), and masked any long-term changes in biomass that occurred during 1968-72.

For this reason, catch and CPUE data can be used to study migration patterns and seasonal availability only if they are based on a large quantity of trawling effort, carried out more or less continuously. The data from the Washington trawl fleet seem well suited to this purpose, since these trawlers spend a great deal of time searching out and catching Pacific ocean perch. *Sebastes alutus* is frequently the target species for this fleet, and made up 29% of its total coastal landings during 1967-71.

In this section, catch and effort data from the Washington trawl fleet will be used to describe migration patterns and seasonal trends in the availability of *S. alutus*. Data on sex and length composition of the catch will also be brought into the analysis, since it is difficult to interpret trends in availability without them.

Queen Charlotte Sound

Seasonal Patterns for the Region

The continental shelf is steep and untrawlable seaward of 150 fm (274 m) in Queen Charlotte Sound, so the fish in this area are inaccessible to trawlers when they move into deep water (January-April). Examination of gonads indicates that spawning occurs in March (Gunderson 1971), but there is no certainty as to where this occurs. Few fish are caught during January-April, and virtually all of these are males (Figure 5) that do not participate in the spawning migration.

Males precede females in their return from wintering areas, and when the fishery first begins in earnest (May), males constitute 68% of the catch. The availability of females increases sharply after May, and by July they dominate the catches.

During June-August, Pacific ocean perch are at the shallowest point in their bathymetric cycle. Catches are low during this period, and large quantities of fish 35 cm or smaller are landed (Figure 6).

Both catch and CPUE rise in September, and although the mean depth of catch is about the same as in July and August, there is a sharp increase in the proportion of fish larger than 35 cm in the catch. Aggregations of large adults must suddenly become available during September, probably because mating activities are beginning.

FIGURE 5.—Mean monthly catch, catch per hour, mean depth of catch, and sex ratio for the Washington trawl fleet during 1967-71. Data for the QCS and WVI stocks of Pacific ocean perch are presented separately.

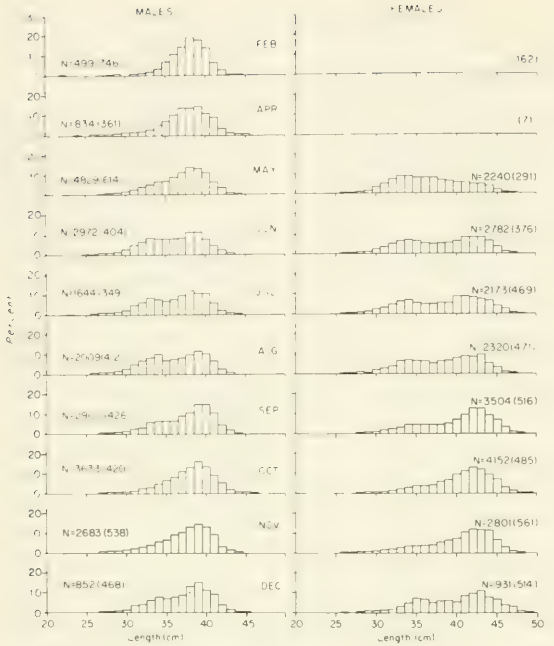

FIGURE 6.—Size composition of 1967-71 Pacific ocean perch catches from Queen Charlotte Sound, by month. Mean numbers caught per hour during 1967-71 are shown in parentheses.

Previous work (Gunderson 1972) has shown that these aggregations are faster growing, but only slightly older, than the rest of the stock.

Pacific ocean perch move into progressively deeper water during October-December, as they return to deepwater spawning areas. Catch per hour remains high during this period, but deteriorating weather conditions force a decline in trawling effort and landings.

Because catch, CPUE, sex ratio, length composition, and age composition all varied with season, the data from different time periods were treated independently in much of the later analysis. The time periods utilized were January-April, May, June-August, and September-December.

Seasonal Patterns for Specific Grounds

The geographic distribution of the catch varied from month to month (Figure 7) and there is a possibility that between-ground variations in size composition could contribute to the results shown in Figure 6. Length and age composition data were analyzed by fishing ground (Figure 8) to examine this point further. To insure that the data used were as typical as possible of the grounds in question, only samples from characteristic fishing depths were chosen for this analysis. The 1967-71 mean depth of catch was computed for each month and ground in question, and only those samples whose range was within 15 fm (27 m) of this mean were analyzed.

The results (Figure 9) show that within a given time period, length composition differed somewhat between grounds, but the differences showed no consistent, predictable pattern. There was no ground that could always be characterized as having larger or smaller fish than the other grounds. Size composition data for SE Corner, SW Corner, and Triangle grounds, the three major fishing grounds, showed only slight between-ground heterogeneity within any given time period.

Washington-Vancouver Island

Unlike Queen Charlotte Sound where the continental shelf drops off abruptly past 150 fm (274 m), a wide range of depths can be fished off Washington and Vancouver Island (Figure 5). Trawlers can follow fish in this area into deepwater spawning areas, and exploit them year around. The year can be divided into a

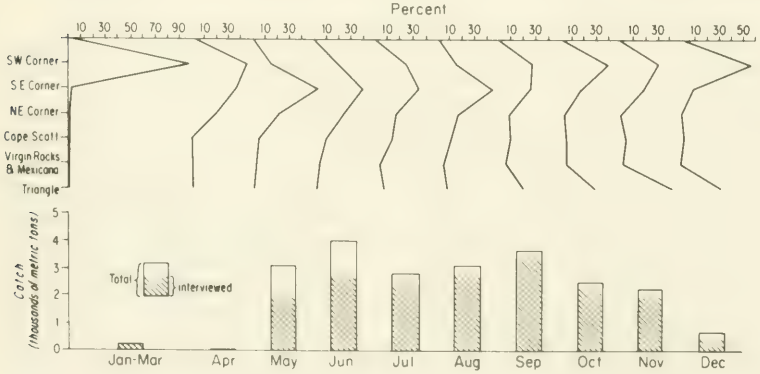

FIGURE 7.—Distribution of 1967-71 Pacific ocean perch catch from Queen Charlotte Sound by month and fishing ground. Data on distribution by ground were derived from the portion of the catch for which fishermen interviews were available. The Virgin Rocks-Mexicana ground includes Virgin Rocks and all grounds east of the Cape Scott ground.

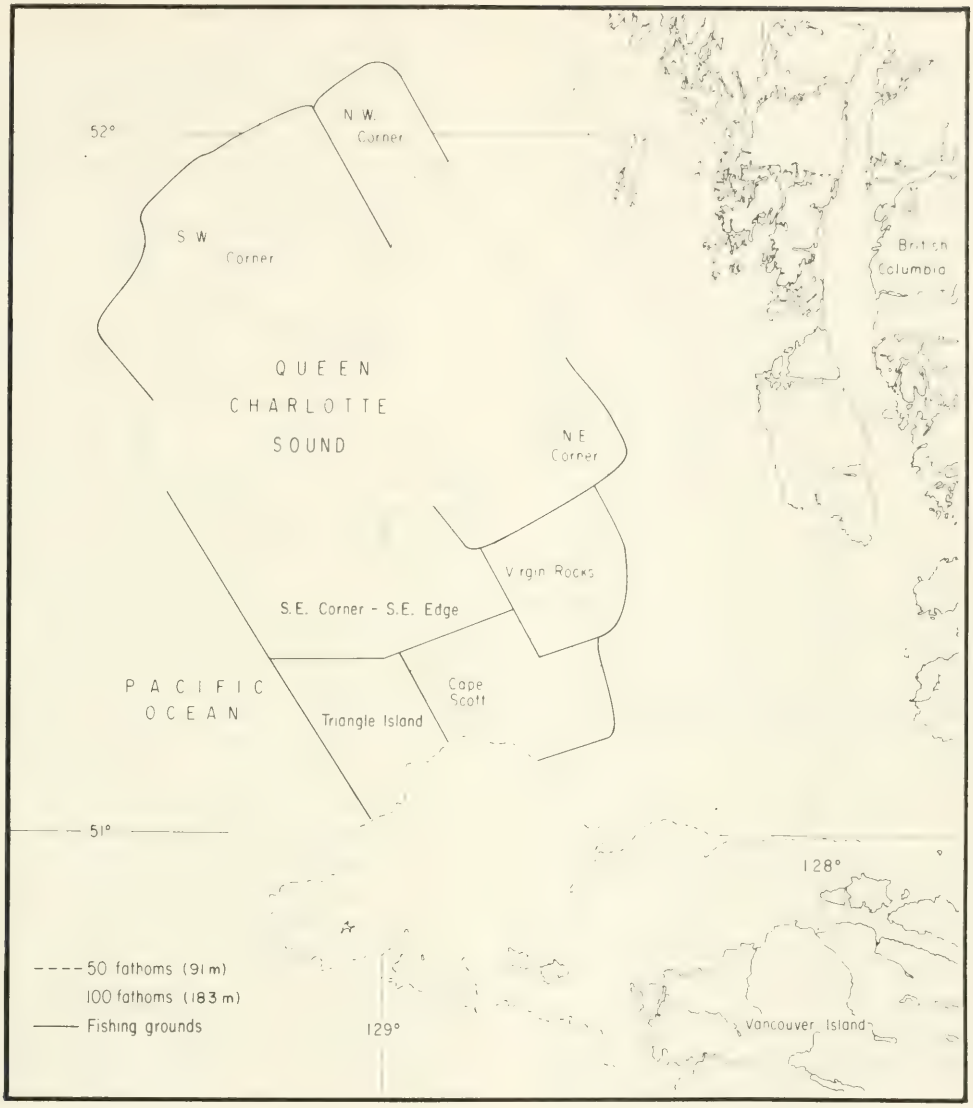

FIGURE 8.—Major Pacific ocean perch fishing grounds in Queen Charlotte Sound, B.C.

November-May period when most of the fish are in deepwater spawning areas, and a June-October period when they are in shallow water. Mean depth of catch is 140-180 fm (256-329 m) during the November-May period, and 120-130 fm (219-238 m) during June-October.

Seasonal variability in the biological composition of the catch is less significant than in Queen Charlotte Sound, since the sex ratio is close to 50% males all year. Data on the size composition of the catch was quite limited during certain months, but size composition generally seemed to depend on the depths at which the fishery was operating. The proportion of small fish (35 cm or smaller) in the landings was highest during the shallow-water fishery, and decreased during November-May (Figure 10).

Considering the wide differences in the magnitude of the landings between Washington-Vancouver Island and Queen Charlotte Sound, CPUE levels are surprisingly similar (Figure 5). Results of research cruises have shown that the availability of Pacific ocean perch varies widely in the Washington-Vancouver Island region (Gun-

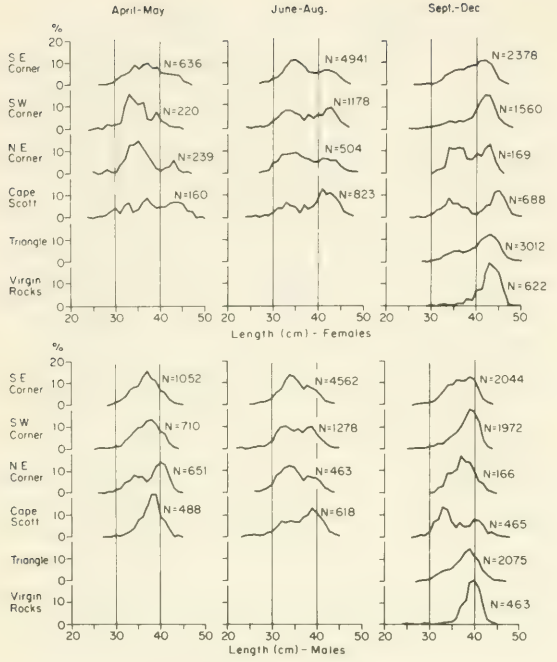

FIGURE 9.—Size composition of 1966-72 Pacific ocean perch catches in Queen Charlotte Sound, by fishing ground and season.

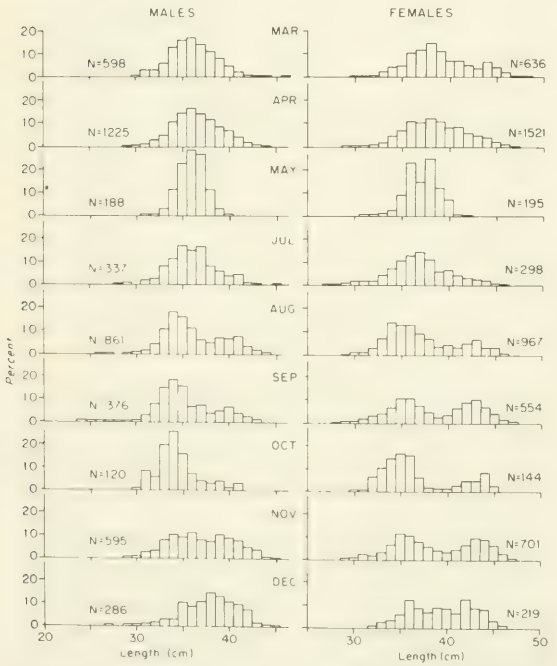

FIGURE 10.—Size composition in 1967-71 Pacific ocean perch catches from Washington-Vancouver Island, by month.

derson 1974), and fishermen probably restrict their efforts to periods of high availability. If this is the case, the relative levels of monthly catch give the best index of stock availability. Peak availability occurs during March-April (near the time of embryo release) and in August-December (near the mating period). This pattern of seasonal availability agrees well with results from previous studies of the WVI stock (Gunderson 1971; Snytko 1971).

AGE-LENGTH RELATIONSHIPS

Queen Charlotte Sound

The age-length relationship in any sample of Pacific ocean perch from Queen Charlotte Sound is influenced by the availability of large, fast-growing fish, the depth at which the fish were captured, and the proportion of the annual growth completed. In order to examine the relative importance of these factors, analysis similar to that outlined by Gunderson (1974) was employed.

This involved fitting observed mean length at age data to the von Bertalanffy growth model,

$$l_t = L_\infty(1 - \exp{-K(t - t_0)})$$

where l_t = length of fish in centimeters at t years
L_∞ = theoretical asymptotic length
K = constant expressing the rate of approach to L_∞
t_0 = theoretical age at which $l_t = 0$.

The least squares technique of Tomlinson and Abramson (1961) was employed to do this, and a separate age-length relationship was computed for each combination of fishing ground and season (April-May, June-August, and September-December) where adequate data were available. All comparisons of the age-length relationship at different grounds and seasons could then be made by comparing fitted length at some common age (age 15 in this case).

The results (Figure 11) show that the age-length relation is more dependent on the availability of fast-growing fish to bottom trawls than on any other factor examined. The main line of evidence supporting this is the close correspondence between changes in fitted length at age 15 (Figure 11) and seasonal changes in size composition (Figure 9), a situation that would be expected if both depend on the availability of large, fast-growing

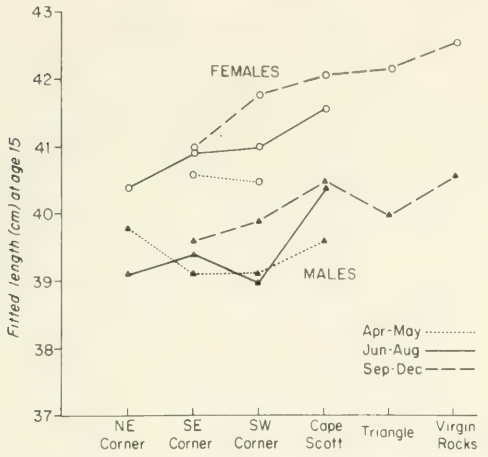

FIGURE 11.—Fitted length at age 15 for Pacific ocean perch in Queen Charlotte Sound (1966-72), by fishing ground, season, and sex.

fish. Both age-length and size composition data indicate that aggregations of these fish are least available during April and May, and that it is only during September-December that they are fully available on all fishing grounds. This general pattern seemed to hold throughout Queen Charlotte Sound, at least on the major fishing grounds. In some instances, however, availability of large, fast-growing fish was unusually high on a relatively minor fishing ground. This seemed to be the case at NE Corner during May and Cape Scott during June-August (Figures 9, 11).

Sampling problems caused by disporportionate fishing intensity in extremes of the bathymetric range are usually insignificant compared with the problems caused by differential availability. Research cruises have shown that mean length at age decreases as depth increases (S. J. Westrheim, pers. commun.), so that fitted length at age 15 should either remain constant (if fishery shifts in response to stock location) or decrease (if fishery shift is independent of stock location) as the fishery shifts to deeper water during September-December (Figure 5). Instead, mean length at age actually increases during September-December (Figure 11) because this is the season when large, fast-growing fish are most available.

Considering all sources of data on catch, CPUE, and biological composition of the landings, it is apparent that there is a significant increase in the size of the exploitable population inhabiting Queen Charlotte Sound during September-December. Age-length data collected during January-August consequently apply to only a fraction of the known population in Queen Charlotte Sound. If it is assumed that all Pacific ocean perch are fully vulnerable to fishing by fall, however, the September-December market sampling data can be taken as representative of the exploitable segment of the QCS stock.

Consequently, 1967-71 age-length data from September-December market samples were used to estimate growth parameters for the QCS stock. Queen Charlotte Sound was treated as a unit, mean length at each age was determined by sex, and the resulting data were fitted to the von Bertalanffy growth model. Both the original data and fitted mean length at age are shown in Table 3.

Washington-Vancouver Island

Availability of Pacific ocean perch in this region influences the age-length relationship, but in a different manner than in Queen Charlotte Sound. Results from research surveys off northern Washington (Gunderson 1974) suggest that mean length at age actually decreases with increasing availability, rather than increasing. The highest rates of catch in this region were obtained when aggregations of large, old, slow-growing fish were most available.

The WVI and QCS stocks also differ substantially in the degree to which mean length at age varies with depth. In contrast to Queen Charlotte Sound, mean length at age has been shown to decrease sharply as depth increases off Washington and Vancouver Island (Westrheim 1973; Gunderson 1974). The decline is so sharp, in fact, that Westrheim (1973) has suggested that there are separate shallow and deepwater stocks in this region.

It is clear, then, that both depth of fishing and availability must be taken into consideration in order to arrive at an age-length relationship that characterizes the WVI stock. Research cruise data obtained off the coast of northern Washington (Gunderson 1974) are particularly well suited to do this, since age-length relationships and availability were systematically observed throughout the bathymetric range. Availability varied widely during these cruises, and, as previously mentioned, this phenomenon masked any long-term changes that occurred during 1968-72. Availability was maximal during the July 1972 cruise, however, and the results from that cruise were used to represent growth in the WVI stock.

TABLE 3.—Number of age-length observations, mean length (centimeters), and fitted length at each age for QCS and WVI stocks of Pacific Ocean perch.

	QCS stock						WVI stock					
	Males			Females			Males			Females		
Age	Number of observations	Mean length	Fitted length	Number of observations	Mean length	Fitted length	Number of observations	Mean length	Fitted length	Number of observations	Mean length	Fitted length
2							3	18.0	18.1	2	18.5	19.1
3							1	22.0	21.2	1	22.0	21.6
4							10	23.7	23.9	11	24.5	24.0
5	8	27.0	26.6	4	26.2	26.0	18	25.8	26.3	6	26.5	26.1
6	19	29.1	28.6	26	29.4	28.4	9	28.3	28.4	10	28.1	28.0
7	70	30.0	30.5	73	30.6	30.6	8	29.6	30.2	5	28.5	29.8
8	164	31.6	32.2	124	32.1	32.6	34	32.3	31.8	21	31.4	31.4
9	186	33.1	33.6	173	33.5	34.3	58	33.2	33.2	22	33.2	32.9
10	219	34.4	35.0	213	34.8	35.9	123	34.2	34.4	71	34.6	34.3
11	233	36.1	36.1	179	36.3	37.2	172	35.5	35.5	123	35.7	35.5
12	411	37.4	37.1	253	38.3	38.5	78	36.3	36.5	89	36.5	36.6
13	463	38.5	38.0	374	40.0	39.6	42	37.0	37.3	72	37.6	37.6
14	417	39.4	38.9	459	41.2	40.6	59	38.0	38.0	57	38.0	38.6
15	308	40.1	39.6	468	42.2	41.4	56	38.9	38.6	58	39.0	39.4
16	203	40.5	40.2	377	43.2	42.2	50	39.7	39.2	61	40.8	40.2
17	116	41.1	40.8	308	43.6	42.9	37	40.2	39.7	75	41.3	41.0
18	80	41.1	41.3	186	44.0	43.6	24	40.8	40.1	52	41.7	41.6
19	30	41.6	41.7	115	44.4	44.1	29	41.1	40.5	36	42.2	42.2
20	14	41.9	42.1	92	44.2	44.6	16	41.3	40.8	30	42.4	42.7
21	13	41.9	42.5	36	45.1	45.0	7	41.4	41.1	14	43.7	43.2
22				10	45.0	45.4	2	39.0	41.4	16	43.6	43.7
23				3	45.3	45.8				7	43.9	44.1
24				7	45.6	46.1				4	44.5	44.5
	von Bertalanffy growth function parameters											
L_∞	45.25			48.75			43.15			48.47		
K	0.1192			0.1135			0.1320			0.0908		
t_0	−2.4157			−1.7159			−2.1186			−3.5041		
SE of estimate	0.44			0.64			0.68			0.45		

Data from the 120-, 160-, and 200-fm (219-, 293-, and 366-m) sampling stations were combined by weighting the mean length at each age by the catch rate of Pacific ocean perch in that depth stratum and arriving at an overall weighted mean length for each age group (Table 3). The calculations were carried out separately for males and females, and the resulting age-length data were then fitted to the von Bertalanffy growth model using the technique described previously.

The results (Table 3) suggest that fish off Washington grow somewhat slower than those in Queen Charlotte Sound. In order for the results from the two stocks to be strictly comparable, however, several research cruises should have been made in Queen Charlotte Sound during September-December. The age-length data from those cruises where availability was maximal could then have been weighted in proportion to the catch rate for each depth stratum, as was done for the WVI stock. If fishermen effectively "sample" in proportion to abundance, however, the results from commercial fisheries data should agree well with those from research cruises.

ANNUAL CHANGES IN SIZE AND AGE COMPOSITION

Size Composition

Queen Charlotte Sound

The Washington State Department of Fisheries has obtained size composition data on landings from Queen Charlotte Sound since 1956. Collection of such data was limited and sporadic prior to

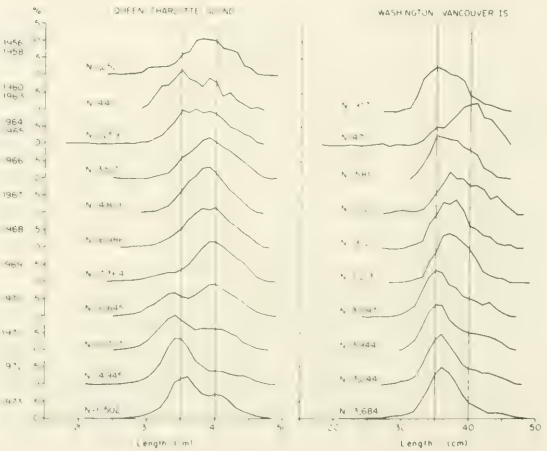

FIGURE 12.—Changes in the size composition (sexes combined) of Pacific ocean perch in commercial catches, 1956-73. N = number of fish sampled.

1967, but a good series of data, taken over the entire year, is available for each year during 1967-73.

Because a limited number of samples was available during 1956-66, it was frequently necessary to pool data from adjacent years when examining temporal trends in size composition. The results (Figure 12) furnish the only available estimates of the size composition of Pacific ocean perch in 1956-66 Washington trawl landings.

Collection of biological data was quite intensive during 1967-73, and it was possible to make allowances for the extensive seasonal changes in length and sex composition that occur in Queen Charlotte Sound. The Sound was treated as a single geographic unit, but size composition was determined separately for each of the four time strata previously discussed (January-April, May, June-August, and September-December). If few landings were made in one of these strata, it was combined with an adjacent stratum, and biological data from the latter were used to represent it. Table 4 shows the time strata used for each year's catch data, the landings in each stratum, and the amount of biological data collected.

Males and females differ in relative abundance and size composition, so they were treated separately. Mean weights of males and females in each time stratum were obtained by employing the length-weight relation (sexes combined) reported by Westrheim and Thomson (1971), together with the appropriate length frequencies in that stratum. The number of males and females landed in each stratum could then be estimated by dividing total pounds landed by the mean weight of fish in that stratum. These values were combined with size composition data to obtain the number of fish landed by time period, sex, and size group. Pooling these data by year and expressing the results in terms of percent frequency yielded the results shown in Figure 12.

TABLE 4.—Time strata used for analysis of 1966-73 size and age composition data from Queen Charlotte Sound. Pacific ocean perch catch by Washington trawlers (metric tons) and amount of biological data collected in each stratum are also shown.

Year	Time stratum	Washington trawl catch	Origin of biological data	Number of fish sampled for	
				Length-sex	Age
1966	Sept.-Dec.	2,723	Oct.-Dec.	3,517	1,419
1967	Mar.-May	868	May	1,104	433
	June-Aug.	2,817	June-Aug.	1,049	848
	Sept.-Dec.	1,656	Sept.-Dec.	2,648	1,183
1968	Jan.-Apr.	220	Jan.-Apr.	1,470	680
	May	842	May	1,310	505
	June-Aug.	1,870	June-Aug.	1,165	608
	Sept.-Dec.	1,855	Sept.-Nov.	3,041	1,011
1969	Jan.-May	687	May	648	298
	June-Aug.	2,205	June-Aug.	2,461	698
	Sept.-Dec.	2,099	Sept.-Dec.	4,255	714
1970	Jan.-May	546	Apr.-May	2,435	498
	June-Aug.	1,749	June-Aug.	4,214	649
	Sept.-Dec.	2,014	Oct.-Dec.	3,996	497
1971	Apr.-Aug.	1,446	May-Aug.	6,974	1,004
	Sept.-Dec.	1,480	Sept.-Dec.	3,733	1,232
1972	Apr.-May	379	May	3,174	887
	June-Aug.	1,568	June-Aug.	7,337	2,587
	Sept.-Dec.	1,417	Sept.-Nov.	4,434	1,321
1973	Mar.-Apr.	530	Apr.	2,940	942
	May	244	May	1,201	398
	June-Aug.	1,019	June-Aug.	5,058	1,658
	Sept.-Dec.	472	Sept.-Nov.	2,303	803

Substantial quantities of large Pacific ocean perch were present in Queen Charlotte Sound during 1956-58. Subsequent changes in size composition reflect changes caused by the commercial fishery and by recruitment of two strong series of year classes. The first series of year classes was centered around the 1952 year class and included the 1951-53 brood years (Westrheim et al. 1972). The presence of this series first became apparent in the 1960-63 landings, when the modal size was 35 cm—corresponding to an age of about 10 yr. The 1952 year class series caused the modal size to move progressively toward the right during 1960-70 (as its members grew in length), but seemed to have little influence on size composition in subsequent years. This is probably the cumulative result of large fishery removals during 1965-69, when the 1952 year class would have been 13-17 yr old.

A second series of strong year classes, centered around the 1961 and 1962 brood years (Westrheim et al. 1972) first showed up in the 1970 landings, when there was a secondary mode at 34 cm. This series of year classes came to dominate the landings during 1971-73, since the abundance of older fish had been drastically reduced by commercial fishing.

Washington-Vancouver Island

Size composition data from this region were more limited than data from Queen Charlotte Sound and it was never possible to analyze different time strata separately. All size composition data were summarized by year to produce the data in Figure 12. Data from 1956 to 1965 were especially limited and size composition data from adjacent years frequently had to be combined. This was done in such a manner that direct comparisons with Queen Charlotte Sound could be made.

Research surveys during 1965 (Westrheim

1970) suggested that the 1952 year class dominated here, as well as in Queen Charlotte Sound, and the results (Figure 12) tend to support this conclusion. The modal size was 35 cm for the 1960-63 period, and this corresponds to an age of about 10 yr. The 1966-67 size composition data also reflect the presence of a strong 1952 year class series, but is is not possible to follow the series past 1967. Extensive fisheries removals during 1966-68 resulted in sharply attenuated right-hand limbs for 1968-73 size composition curves, and the 1952 year class series was presumably swallowed up in these removals.

As in Queen Charlotte Sound, the strong 1961-62 year class series first showed up on the 1970 landings, when there was a mode at 35 cm. Because the biomass of older fish had been drastically reduced by the extensive fisheries removals of 1966-68, these year classes dominated the catches in the first year they appeared and in each subsequent year.

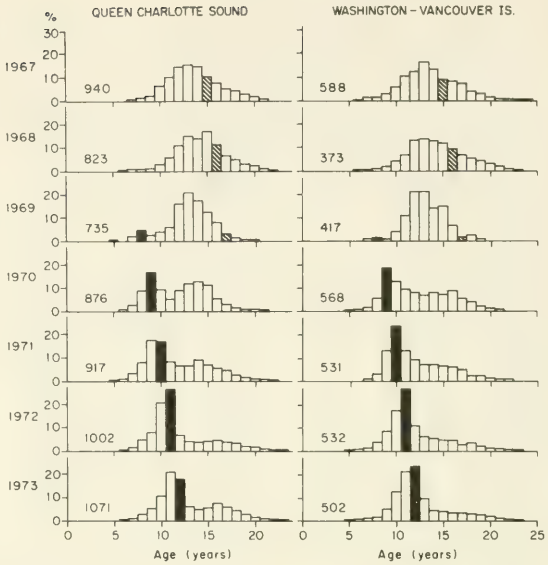

FIGURE 13.—Changes in the age composition (sexes combined) of Pacific ocean perch in commercial catches, 1967-73. The number of fish caught per hour is shown for each year, and the 1952 and 1961 year classes have been indicated by shading.

Age Composition

Queen Charlotte Sound

Age composition data for the Washington trawl landings from Queen Charlotte Sound have been collected since 1966. A series of data taken over the entire year is available for each year during 1967-73.

The procedure used to estimate the age composition of the 1967-73 landings was identical to that employed in the section on size composition. The number of fish landed in each time stratum was combined with the age-frequency data for that stratum to estimate the number of fish landed by age-group, sex, and time stratum. Pooling these data by year and dividing by the total Washington trawl effort expended in Queen Charlotte Sound yielded annual estimates of the number caught per hour, by age-group, and of percent age composition (Figure 13).

The 1952 year class series was centered around age 13 in 1965 and was almost fully vulnerable to fishing when the Queen Charlotte Sound fishery began its dramatic expansion. The cumulative effects of the extensive removals of 1966-67 were such that the 1951-53 year classes no longer dominated the catches after 1967-68. The 1952 year class series was exploited far more intensively than preceding year classes, and by the time the 1951-53 year classes were 17-19 yr old, they were less abundant than the relatively weak 1948-50 year classes had been at corresponding ages. This can be seen by comparing the abundance of 17-19 yr olds in 1970 (45 fish caught per hour) with their abundance in 1967 (118 fish caught per hour).

During 1970 and 1971, recruitment of the strong 1961 and 1962 year classes to the fishery restored the abundance of Pacific ocean perch to 1967 levels (Figure 13) and the number of fish caught per hour continued to increase through 1973. The condition of the QCS stock in 1973 was far from satisfactory, however, since it was made up of much younger fish than those characterizing even the 1967 stock.

Washington-Vancouver Island

No age composition data were available for Pacific ocean perch catches from the WVI stock until 1966, and it was not until 1967 that an adequate series of age composition samples was collected (Table 5). Age composition data on the WVI catches were quite limited, so no attempt was made to treat different time strata separately.

Age composition data for 1967-73 are remarkably similar to corresponding data from Queen Charlotte Sound (Figure 13). The harvests of 1966-68 sharply reduced the biomass of the 1952

TABLE 5.—Number of Pacific ocean perch from the WVI stock sampled for biological data.

Year	Length-sex	Age	Year	Length-sex	Age
1966	581	216	1970	3,089	1,124
1967	1,020	707	1971	3,944	1,460
1968	912	502	1972	3,044	1,036
1969	1,213	296	1973	3,684	1,335

year class series, which would have ranged from about 13 to 15 yr of age in 1966 and would have been almost fully vulnerable to trawling. Recruitment of the 1961 and 1962 year classes to the fishery began to restore abundance (as indicated by the number caught per fishing hour) to former levels and, as of 1970, the WVI stock was on the road to recovery. After 1970, however, the condition of the WVI stock followed an entirely different course than the QCS stock.

Exploitation rates for the QCS stock were low enough to allow an increase in abundance (number caught per hour) during 1970-73 (Figure 13), as the 1960-61 year classes became fully available to the fishery. Off Washington and Southwest Vancouver Island, however, exploitation rates remained at high levels during 1970-73, and the 1961-62 year classes were cropped off as soon as they recruited to the fishing grounds. Abundance consequently declined during 1970-73, opposite to the trend in Queen Charlotte Sound. The abundance of fish 15 yr and older was reduced below even 1970 levels, and 10 to 13 yr-old fish dominated the WVI stock as of 1973.

RECRUITMENT TO THE FISHERY

Consideration of the length-maximum girth data presented by Westrheim and Nash (1971) indicates that gear selection should begin at a relatively small size. The internal (between-knot) measure of the cod end mesh size commonly used by Washington trawlers is about 3.25 inches (8.26 cm) and the smallest fish retained should have a girth of $2 \times 3.25 = 6.5$ inches. This assumes that escape is not facilitated by compressability on the one hand and that the rigidity of the trawl meshes does not hinder escape on the other. If these assumptions are valid, and the girth at 50% retention is 6.5 inches, Westrheim and Nash's results show that the 50% selection length should be 24.5 cm.

A 25.4-cm fish would be too small for market acceptance, but previous comparisons of Pacific ocean perch size composition in research catches and commercial landings (Gunderson 1972) have indicated that 50% of all 32- to 34-cm fish on the grounds are retained by Washington trawlers. Virtually all fish 36 cm and larger are retained by the fishermen. Reference to the age-length information in Table 3 shows that the length at 50% retention corresponds to an age of about 8 or 9 yr, and that all fish older than 11 yr would be retained. Slight between-stock differences in retention would be expected, owing to differences in growth rate.

Despite the fact that all fish older than age 10 are vulnerable to the fishing gear in use, and large enough that almost all are retained for market sales, age composition data from commercial catches (Figure 13) and research surveys (Gunderson 1974) show that recruitment to the fishing grounds is not complete until much later than age 10. On the assumption that the modal age of the catch lies near the first year in which recruitment is complete, these data would imply that full recruitment could occur anywhere from age 11 to 14.

The high variability in modal size is caused by year to year variation in availability, year class strength, and fishing mortality, and one way to reduce its significance is to deal with long-term averages of relative abundance. In order to do this, a relative abundance index (U_i) was calculated for each age group using the 1967-73 age composition data for the QCS and WVI stocks. This index was calculated as:

$$U_i = \frac{1}{7} \sum_{n=1967}^{1973} \left(\frac{C}{f}\right)_n$$

where U_i = the relative abundance of the ith age-group and $\left(\frac{C}{f}\right)$ = the number of fish in the ith age-group caught per hour. Percentage age composition during 1967-73 has been calculated from these U_i data and is shown by stock in Figure 14.

The results show that although the modal age in both stocks is 11 yr, recruitment to the fishing grounds is quite gradual. In fact, it is not until age 15 that the full force of fishing mortality seems to be exerted on any given year class. Estimates of the exact proportion of the fish in each age-group that have recruited to the fishing grounds, and are vulnerable to fishing, can be derived from U_i values, starting with the relation:

$$C_i = uV_iN_i$$

where C_i = catch of fish in the ith age-group

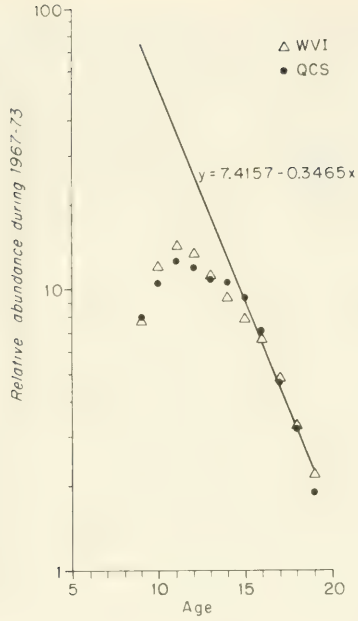

FIGURE 14.—Relative abundance of age groups 5-19 during 1967-73, for the QCS and WVI stocks of Pacific ocean perch.

u = exploitation rate
V_i = proportion of population vulnerable at age i
N_i = total number of fish in the ith age-group.

Similarly, $C_{t-1} = uV_{t-1}N_{t-1} = uV_{t-1}N_t \exp -(V_t F + M)$ if we assume that V_i remains constant throughout the year, and:

$$\frac{U_t}{U_{t+1}} \approx \frac{C_t}{C_{t+1}} = \frac{V_t}{V_{t-1} \exp -(V_t F + M)}.$$

This equation can be solved iteratively for V_i if we have estimates of F (fishing mortality), M (natural mortality), V_{i+1}, and the ratio U_i/U_{i+1}.

The estimates of Z (total instantaneous mortality) and F were derived directly from the data in Figure 14. Trends in the relative abundance of 15-19 yr olds were quite similar in the QCS and WVI stocks, and Z was estimated by fitting a common regression line to the data for both stocks. The resulting regression equation for 15-19 yr olds was:

$$\log Y = 7.4157 - 0.3456X,$$

where Y = relative abundance during 1967-73, expressed as percent frequency
X = age in years.

The slope of this line (0.35) was used to represent Z for fully recruited age-groups. This was then separated into F and M by assuming a known value for M.

Estimation of V_i schedules began by assuming that the vulnerability coefficient for 16 yr olds (V_{16}) was 1.0. Using the QCS data, and $M = 0.12$ for example:

$$\frac{U_{15}}{U_{16}} = 1.31 = \frac{V_{15}}{1.0 \exp -(0.23\ V_{15} + 0.12)}.$$

By iteration, it was determined that $V_{15} = 0.94$ and this value was used to determine V_{14} from:

$$\frac{U_{14}}{U_{15}} = 1.14 = \frac{V_{14}}{0.94 \exp -(0.23\ V_{14} + 0.12)}.$$

Again this was solved iteratively, giving $V_{14} = 0.79$. Proceeding backwards, the vulnerability coefficients for Queen Charlotte Sound were estimated for all age-groups 10 and older. The calculations could not be carried past age 10, since younger age-groups may be subject to substantial rates of discard by fishermen.

Estimates of the V_i schedules for both the QCS and WVI stocks are shown in Table 6. Calculations were carried out for $M = 0.15$, $F = 0.20$ as well as for $M = 0.12$, but this had little effect on the estimates of vulnerability. The geometric means of the vulnerability coefficients obtained by assuming different values of M have been plotted graphically in Figure 15 and suggests that the proportion recruited to the fishery is a linear function of age. There is no obvious reason why this should be so, however, and no attempt was made to fit a straight line (or lines) to these data, or to extend the relationship to fish less than 10 yr old. The geometric means of the V_i estimates were used directly in all later work.

TABLE 6.—Proportion of Pacific ocean perch population vulnerable to fishing, by age-group and stock.

Stock	M	10	11	12	13	14	15	16
QCS	0.12	0.32	0.45	0.53	0.62	0.79	0.94	1.00
	0.15	0.30	0.43	0.52	0.61	0.78	0.94	1.00
	Mean	0.31	0.44	0.53	0.62	0.79	0.94	1.00
WVI	0.12	0.36	0.53	0.64	0.69	0.75	0.87	1.00
	0.15	0.34	0.51	0.63	0.68	0.75	0.87	1.00
	Mean	0.35	0.52	0.64	0.69	0.75	0.87	1.00

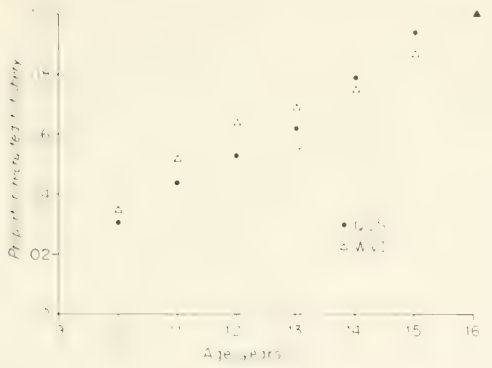

FIGURE 15.—Estimated proportion of each age group recruited to the fishing grounds, for the QCS and WVI stocks of Pacific ocean perch.

MORTALITY

All estimates of Pacific ocean perch mortality rates depend on a knowledge of the age structure of the population. Virtually all fish caught die from the effects of decompression, so that no successful tagging studies have ever been carried out.

In this section, data on number caught per hour by age-group were used to estimate the survival of 14- to 18-yr-old Pacific ocean perch in year n to ages 15-19 in year $n + 1$, or to ages 16-20 in year $n + 2$. These age-groups were chosen so as to strike a balance between problems with incomplete recruitment on the one hand and age determination problems on the other. Previous analysis has suggested that recruitment is not complete until age 16, about the same time that age determination becomes difficult (Table 7) and the ages of some individuals are presumably underestimated. No age-groups older than 20 should be included in survival estimates, and restricting mortality estimates to fully recruited age-groups (16-19 yr olds) could result in underestimation of survival rates. Inclusion of the incompletely recruited 14 and 15 yr olds offset this to some degree and had the additional benefit of basing the survival estimates on five age-groups rather than three.

All survival estimates were expressed on an annual basis (S), and then used to estimate Z. On the assumption that M is density independent and that F is a linear function of total hours trawled, the model $Z = q\bar{f} + M$, where q = proportion of population caught by trawling 1 h and $\bar{f}$ = mean annual number of hours trawled, was employed. Linear regression of Z on $\bar{f}$ yields estimates of q and M where the model is appropriate.

Total international fishing effort (f) was estimated by dividing the total international catch in a given year by the corresponding CPUE for the Washington trawl fleet (after Gulland 1969). The value of $\bar{f}$ was obtained by averaging f over the years that each estimate of Z pertained to.

Queen Charlotte Sound

Calculation of total international fishing effort is outlined in Table 8. The 1967-72 Soviet catch data for the INPFC Charlotte area was taken from unpublished analyses by T. A. Dark and N. B. Parks. These data were derived from analysis of fleet location and catch by quarter and give the most detailed breakdown of the Soviet catch that is currently available. Soviet catch estimates for 1965, 1966, 1972, and 1973, as well as all Japanese and North American data for the years 1963-73, were derived from Westrheim et al. (1972) and a recent update of that report.

Estimates of Z are plotted against mean international fishing effort (Table 8) in Figure 16 and the results indicate that the information collected so far can provide only tentative estimates of M. Pacific ocean perch vary widely in their availability to on-bottom trawls and the CPUE indices used in mortality estimation are consequently suscep-

TABLE 7.—Deviations of Canada's final otolith readings from those of United States, by age-group, for a collection of Pacific ocean perch from Queen Charlotte Sound, June 1972.[1]

Deviations from Washington	1	2	3	4	5	6	7	8	9	10	11	12	14	15	16	17	18	19	20	22	25	Total	Percent
+5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	—	3	3.6
+4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	2	1	4	4.8
+3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	2	2.4
+2	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	2	—	1	—	—	—	5	6.0
+1	—	—	—	—	—	—	—	—	—	—	3	1	1	2	—	1	—	—	—	—	—	8	9.5
0	6	11	10	4	4	3	1	3	2	9	4	—	—	—	2	—	—	—	—	—	—	59	70.2
−1	—	—	—	—	1	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	3	3.6
Total	6	11	10	4	5	3	1	3	3	11	7	2	1	2	2	4	1	1	2	4	1	84	100.1

[1]S. J. Westrheim and W. R. Harling. 1973. Report on the 1972 comparison of Pacific ocean perch otolith and scale interpretations. Unpubl. manuscr., 24 p.

TABLE 8.—Calculation of total international fishing effort for Pacific ocean perch in Queen Charlotte Sound and the INPFC Vancouver area.

Year	Catch (metric tons) U.S.-Can	Jap.	U.S.S.R.	Total	Washington CPUE (metric tons/hour)	Total international effort (Wash. hours)
			Queen Charlotte Sound			
1963	3,712			3,712	0.841	4,414
1964	3,507			3,507	0.731	4,798
1965	4,889		7,000	11,889	1.040	11,432
1966	8,254	few	18,800	27,054	1.132	23,899
1967	5,745	3,196	17,800	26,741	0.800	33,426
1968	6,051	5,614	1,827	13,492	0.722	18,687
1969	6,628	6,268	55	12,951	0.656	19,742
1970	6,077	3,775	2	9,854	0.714	13,801
1971	4,165	702	few	4,867	0.670	7,264
1972	5,561	2,281	0	7,842	0.710	11,045
1973	3,626	958	0	4,584	0.812	5,644
			Vancouver area			
1966	2,358	few	14,000	16,358	0.640	25,559
1967	805	6,678	10,263	17,746	0.434	40,889
1968	552	4,751	4,602	9,905	0.247	40,101
1969	583	1,787	2,143	4,513	0.242	18,649
1970	1,955	2,186	814	4,955	0.298	16,628
1971	1,155	1,838	1,145	4,138	0.317	13,054
1972	624	1,580	878	3,082	0.312	9,878
1973	344	2,989	490	3,823	0.228	16,768

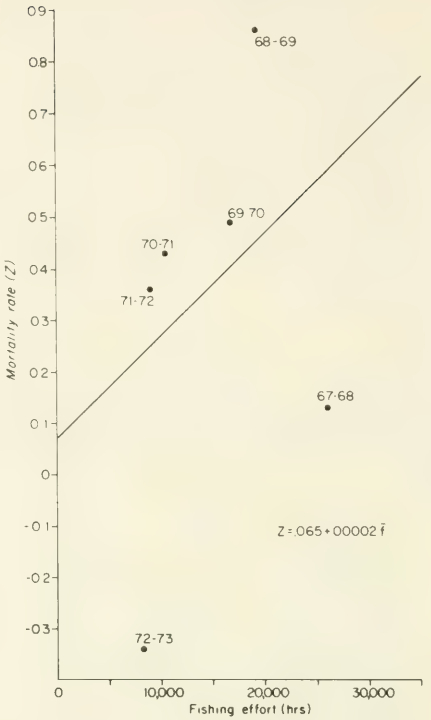

FIGURE 16.—Relation between total instantaneous mortality rate (Z) and fishing effort for the QCS stock of Pacific ocean perch, based on data from the Washington trawl fleet.

tible to fluctuations that have no relation to abundance. Fluctuations of this nature were responsible for much of the variability in Figure 16 and resulted in negative mortality estimates for 1972-73. The low quality of the data on international catch (especially U.S.S.R. data) also contributed to this variability, however.

Linear regression was carried out for the data in Figure 16, and the resulting estimates of M and q were 0.065 and 0.00002, respectively. As expected, correlation between Z and f was quite low (r = 0.30).

Washington-Vancouver Island

Calculation of international effort in the INPFC Vancouver Area is outlined in Table 8. The data sources used to estimate total international effort are the same as for Queen Charlotte Sound.

Annual estimates of Z are plotted against mean international effort in Figure 17. Research cruises off Washington (Gunderson 1974) have shown that extreme fluctuations in the availability of Pacific ocean perch occur here and that changes in the age composition of the catch seem to be associated with them. As in Queen Charlotte Sound, these changes in availability, together with the low quality of the international effort data, generate a high degree of variability in the relation between Z and $\bar{f}$. Correlation between these variables was higher than in Queen Charlotte Sound (r = 0.49), however, and the data seemed to conform more closely to the model proposed. Linear regression analysis resulted in estimates of M = 0.232 and q = 0.00001 for the WVI stock.

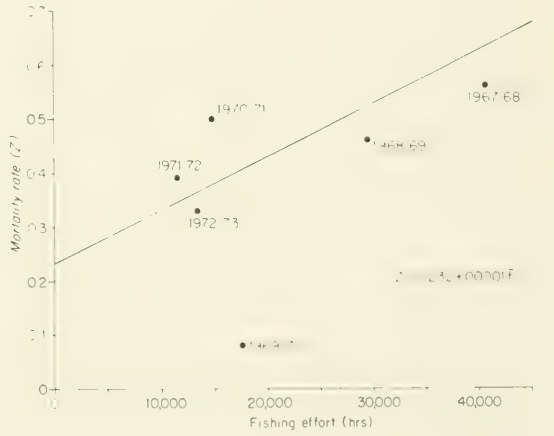

FIGURE 17.—Relation between total instantaneous mortality rate (Z) and fishing effort for the WVI stock of Pacific ocean perch, based on data from the Washington trawl fleet.

The estimate of M obtained for the WVI stock agrees well with an estimate obtained by Chikuni (1975). Chikuni used CPUE and age composition data from the Japanese trawl fleet, and estimated M to be 0.227 for Pacific ocean perch in the Oregon-British Columbia region.

The general applicability of the $Z = q\bar{f} + M$ model for both the QCS and WVI stocks was encouraging and suggests that further collection of data on mortality rates should give increasingly more reliable estimates of M. At present, however, it probably is unwise to overemphasize the between-stock differences found in natural mortality. The results of the current study should be regarded as somewhat tentative and serve mainly to show that M in the Washington-Queen Charlotte Sound region lies in the range between 0.1 and 0.2.

SEXUAL MATURATION

Maturity Criteria Used

Seasonal changes in the gross morphology of Pacific ocean perch gonads have previously been used to describe the reproductive cycle in the Washington-Queen Charlotte Sound region (Gunderson 1971; Snytko 1971). This technique was again employed in this study, and, during 1968-73, 9,548 mature fish were classified as to maturity state using the criteria in Table 9.

Mating and insemination activities cause a reduction in the proportion of males whose gonads are swollen with sperm (Stage 3), and seem to occur during August-September in both the QCS and WVI stocks (Table 10). About 3 mo pass before ovulation and fertilization of eggs occur, and this is first detectable when females in maturity Stage 4 are encountered. Embryonic development begins after fertilization and continues for about 2 mo before embryos are released.

TABLE 9.—Description of the stages used to describe Pacific ocean perch maturity.

Maturity Code	Maturity Stage	Description of gonads
		Males
1	Immature	Stringlike, translucent
9	Maturing	Stringlike, translucent brown or white
8	Resting	Ribbonlike, triangular in cross-section, brown or white
3	Large white	Large and swollen, somewhat rounded in cross-section, glistening white
		Females
1	Immature	Ovary small and translucent
2	Maturing	Ovary small and yellow
3	Large yellow	Ovary firm, oocytes yellowish and opaque
4	Yolk cleared (eggs fertilized)	Ovary not firm, eggs yellowish and translucent
5	Eyed embryos or larvae	Ovary not firm, eggs translucent with black dots or visible larvae
6	Spent	Ovary large and flaccid with a red, purple, or dark gray color
7	Resting	Ovary firm, gray or pink, some with black blotches.

The peak of the embryo-release period occurs during March in the WVI stock (Table 10). Most of the females examined in February were in the "fertilized" stage (Stage 4), while most of those examined during April were in the "resting" stage (Stage 7). Few observations could be made for QCS females during February-April, but the results suggest that embryo release occurs near March. The relatively high proportion of recently spent fish (Stage 6) encountered during May suggests that spawning occurs somewhat later in Queen Charlotte Sound than it does off Washington and southwest Vancouver Island.

Age and size at first maturity should be determined during the period when mature gonads are most fully developed, near August-September for males and near March for females. The central problem in determining length or age at maturity is the status of "maturing" fish (Table 9), and further work was carried out to determine whether or not these fish are sexually mature. Two hundred sixteen fish covering a broad range of lengths were selected from the 1971-72 commercial landings for this purpose. The length (centimeters), sex, and weight (decigrams) of each fish were determined, and the gonads classified as to maturity state. The gonads were then removed from the fish and weighed to the nearest 0.01 g. The results (Figure 18) were expressed in terms of relative gonad weight (g), where

$$g = \frac{\text{gonad weight (grams)}}{\text{body weight (grams)}} \times 10^2$$

i.e.; gonad weight expressed as a percentage of body weight.

Males

Between-season comparisons show that the relative gonad weights of "maturing" males are virtually the same during the mating season (August-September) as they are during March, when all male gonads are in a quiescent state. These fish are obviously immature and seasonal changes in their relative gonad weight contrast sharply with those of adult fish. Fish classified as "maturing" should therefore be grouped with

TABLE 10.—Percentage of adult Pacific Ocean perch in each maturity stage, by stock, during 1968-73.

Item	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.
Males:					QCS Stock						
Total examined		231		339	659	486	279	328	407	430	340
Percent in each maturity stage:											
Stage 8		100		100	99	71	27	58	55	82	100
Stage 3					1	29	73	42	45	18	
Total		100		100	100	100	100	100	100	100	100
Females:											
Total examined		7		11	219	364	212	358	442	675	512
Percent in each maturity stage:											
Stage 3		71		18		18	63	75	99	100	99
Stage 4				9							1
Stage 5				18	1						
Stage 6		14			18	2	2	1			
Stage 7		14		55	80	80	35	25	1		
Total		99		100	99	100	100	101	100	100	100
Males:					WVI Stock						
Total examined		234	223	448			[1]183	151	102		225
Percent in each maturity stage:											
Stage 8		100	100	100			26	32	65		100
Stage 3							74	68	35		
Total		100	100	100			100	100	100		100
Females:											
Total examined	[1]101	197	213	537			[1]129	178	118		210
Percent in each maturity stage:											
Stage 3	30	4	1	1			78	100	100		100
Stage 4	69	63	11								
Stage 5	2	30	43	4							
Stage 6		2	15	14							
Stage 7		1	30	81			22				
Total	101	100	100	100			100	100	100		100

[1]All fish examined during this month came from research vessel catches.

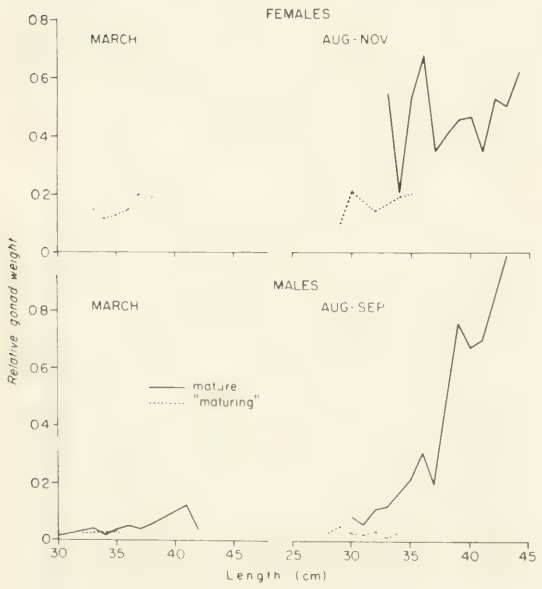

FIGURE 18.—Seasonal changes in the relative gonad weight of mature and "maturing" Pacific ocean perch by length group and sex.

"immature" males in all analysis of length or age at maturity.

There was considerable overlap in the relative gonad weight of mature and "maturing" males during March. Relative gonad weight of adult males examined during the mating season increased exponentially with size, however, so that mature and immature fish were readily differentiated for fish longer than about 32 cm. For smaller fish, however, the relative size of the gonad was not sufficient to determine whether or not a fish was mature, and color had to be relied on to a large degree. If the gonads were white rather than brown, this was taken to indicate the presence of developing sperm and the fish was classified as mature. Whether or not these small males actually participate in mating remains an unanswered question, however.

Because mature and "maturing" males were most readily differentiated when mature fish had white, swollen gonads, only data collected during June-October were used to determine size and age at maturity. The data in Table 10 show that significant quantities of males with Stage 3 gonads were found during this period.

Females

Female gonads are difficult to weigh during the embryo release period, since they are easily ruptured then. Furthermore, eggs and embryos can be extruded with slight pressure on the body cavity during this period, and it is possible that significant quantities of these sex products are lost when fish are compacted in the cod end of a trawl. For these reasons, no data on gonad weight of mature females were taken during March.

Between-season comparisons for "maturing" females (Figure 18) show that their relative gonad weights were virtually the same during August-November as they were during the embryo release period in March. This is conclusive evidence that "maturing" fish are not sexually active, and they were grouped with immature fish in all later analysis.

Differentiation of "maturing" and mature fish was less difficult for females than for males. It was most difficult during July-November, when most adult fish were in maturity Class 3 (Table 10), and had gonads that were similar to "maturing" gonads in color. There was also some overlap in the relative gonad weights of mature and "maturing" individuals of the same length during this period (Figure 18).

During the embryo release period, or when females were in the resting state, adult gonads were readily differentiated from the small, yellowish gonads of "maturing" fish. Consequently, only maturity data collected during February-June were used to examine the size and age at first maturity for females.

Length and Age at Maturity

Data on maturity of Pacific ocean perch have been gathered since 1968, during the course of routine biological sampling of commercial catches. In addition, some maturity data were available from research cruises off the northern Washington coast. The data for 1968-72 combined were examined by stock to determine size and age at maturity.

In most instances, age, length, and maturity data were available for individual fish, and the proportion of mature fish in each cell of an age-length matrix could be calculated. This type of analysis was carried out for both males and females from Queen Charlotte Sound (Tables 11, 12) and for females off Washington and southwest Vancouver Island (Table 13).

Only 213 age-length-maturity observations were available for WVI males, too few to allow direct analysis of maturation by age-groups. Examination of the relation between length and maturity was possible, however, as 551 length-maturity observations were available.

Length-maturity relation

Tables 11 through 13 show the proportion of mature fish in each cell of an age-length matrix. The region in which 50-80% of the fish were mature is delineated by the isopleths drawn in these tables and can be interpreted as a maturity response surface. For all three sets of data, the 50-80% region occupied a narrow range of size groups (3-5 cm) and a relatively wide range of age-groups (5-6 yr). Hence it seems that maturation of both male and female Pacific ocean perch depends more on the size of a fish than its age.

Raw data on length versus proportion mature were plotted for each area and sex (Figure 19) and seemed to conform to a logistic equation (Finney 1971) of the form:

$$P_l = \frac{1}{1 + \exp - \left(\frac{l - l_{0.50}}{\sigma}\right)}$$

where l = length in centimeters
P_l = proportion mature at length l
$l_{0.50}$ = length where: $P_l = 0.5$ = maturation length
σ = constant.

The length-maturity curves are quite steep in the vicinity of $P_l = 0.2$-0.8 and maturation can be regarded as knife-edged, taking place at $l_{0.50}$. Because the above equation is symmetrical about $l_{0.50}$, the area under the curve and to the left of $l_{0.50}$ is equal to the area above the curve and to the right of it. Hence, the errors introduced by assuming knife-edged maturation at $l_{0.50}$ tend to balance.

By algebraic manipulation, the above equation can be linearized to:

$$\ln\left(\frac{1}{P_l} - 1\right) = \frac{l_{0.50}}{\sigma} - \frac{l}{\sigma} .$$

The equation was then in the form $y = \alpha + \beta l$ and

TABLE 11.—Proportion mature in each length and age-group, for female Pacific ocean perch from the QCS stock. Cells with only one observation were not considered.

Length (cm)	5	6	7	8	9	10	11	12	13	14	15	16+	Proportion mature by length	Number examined
22														1
24													0.00	2
25			0.00										0.00	3
26			0.00										0.00	3
27			0.00										0.00	4
28			0.00	0.00									0.00	10
29		0.00	0.00	0.00	0.00								0.00	23
30			0.00	0.00	0.00								0.00	20
31			0.00	0.00	0.00	0.00	0.00						0.00	45
32				0.00	0.06	0.00	0.00	0.05					0.04	79
33			0.00	0.20	0.09	0.04	0.00	0.00					0.07	85
34				0.00	0.03	0.15	0.11	0.25	0.00				0.09	90
35				0.00	0.22	0.48	0.27	0.30	0.00				0.29	85
36				0.00	0.56	0.32	0.28	0.64	0.67	1.00	1.00		0.44	87
37					1.00	0.56	0.92	0.56	0.57	0.83	1.00		0.68	73
38						0.67	0.64	0.83	0.75	0.82	1.00		0.74	53
39							1.00	0.83	1.00	1.00	0.88		0.95	60
40							0.89	1.00	1.00	0.90	1.00	1.00	0.95	66
41								1.00	1.00	1.00	0.95	0.88	0.97	69
42								1.00	1.00	1.00	1.00	0.93	0.99	75
43									1.00	1.00	1.00	1.00	1.00	65
44									1.00	1.00	1.00	1.00	1.00	53
45									1.00	1.00	1.00	1.00	1.00	28
46											1.00	1.00	1.00	11
47												1.00	1.00	4
49														1
Proportion mature by age		0.00	0.00	0.03	0.13	0.25	0.37	0.64	0.81	0.96	0.97	0.95		
Number examined	1	4	35	75	152	143	139	77	116	135	108	110		

TABLE 12.—Proportion mature in each length and age-group, for Pacific ocean perch males from the QCS stock. Cells with only one observation were not considered.

Length (cm)	<4	5	6	7	8	9	10	11	12	13	14	15	16+	Proportion mature by length	Number examined
21															1
23															1
24															1
25														0.33	3
26		0.00		0.00	0.33									0.14	7
27			0.00	0.00										0.00	7
28				0.00										0.00	6
29			0.00	0.00	0.00	0.50								0.10	21
30				0.40	0.25	0.50								0.33	21
31				0.80	0.57	0.61	0.64	0.50						0.61	59
32				0.50	0.61	0.80	0.69	1.00						0.75	67
33					0.69	0.97	0.94	0.92						0.91	113
34				1.00	1.00	0.97	0.93	0.93	0.88	1.00				0.94	166
35					1.00	1.00	0.98	1.00	1.00	1.00	1.00			0.99	150
36						1.00	0.94	0.98	1.00	1.00	1.00	1.00		0.98	157
37						1.00	1.00	1.00	0.98	1.00	1.00	1.00	1.00	0.99	167
38							1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	202
39							1.00	1.00	0.97	1.00	1.00	1.00	1.00	1.00	207
40								1.00	1.00	1.00	1.00	1.00	1.00	1.00	224
41									1.00	1.00	1.00	1.00	1.00	1.00	149
42									1.00	1.00	1.00	1.00	1.00	1.00	77
43											1.00	1.00	1.00	1.00	29
44													1.00	1.00	5
45													1.00	1.00	2
Proportion mature by age		0.00	0.14	0.29	0.56	0.89	0.92	0.97	0.98	1.00	1.00	1.00	1.00		
Number examined	1	5	7	34	94	150	225	230	241	250	217	158	230		

the data in Tables 11-13 could be used in weighted linear regression of $\ln[(1/P_l) - 1]$ on l. The weights used for y observations were $1/\mathrm{Var}(y) = nP_l(1 - P_l)$. Regression coefficients obtained were then used to estimate $l_{0.50}$ $(-\alpha/\beta)$ and σ $(-1/\beta)$.

These estimates were made by sex for Pacific

TABLE 13.—Proportion mature in each length and age-group, for female Pacific ocean perch from the WVI stock. Cells with only one observation were not considered.

Length (cm)	6	7	8	9	10	11	12	13	14	15	16+	Proportion mature by length	Number examined
28		0.00										0.00	3
29												0.00	2
30		0.00										0.00	3
31			0.00									0.00	5
32				0.00	0.00							0.00	7
33			0.67		0.00	0.00	1.00					0.33	15
34				0.40	0.38	0.25	0.57	1.00	0.50			0.44	32
35				0.33	0.59	0.70	0.67	1.00	1.00	1.00		0.65	46
36		1.00		0.67	0.77	0.50	0.92	0.88	0.85	1.00	0.80	0.79	100
37			1.00	1.00	0.75	0.70	0.95	1.00	0.83	0.80	1.00	0.87	105
38				0.75	0.89	1.00	0.86	1.00	1.00	1.00	1.00	0.97	123
39					1.00	1.00	0.88	1.00	0.93	1.00	1.00	0.97	111
40							1.00	1.00	1.00	1.00	1.00	1.00	65
41							1.00	1.00	1.00	1.00	1.00	1.00	69
42									1.00	1.00	1.00	1.00	34
43									1.00	1.00	1.00	1.00	46
44									1.00		1.00	1.00	26
45											1.00	1.00	13
46											1.00	1.00	11
47											1.00	1.00	2
48											1.00	1.00	2
49											1.00	1.00	1
Proportion mature by age	0.33	0.25	0.42	0.46	0.60	0.65	0.87	0.98	0.94	0.98	1.00		
Number examined	3	8	12	24	67	81	101	105	103	98	219		

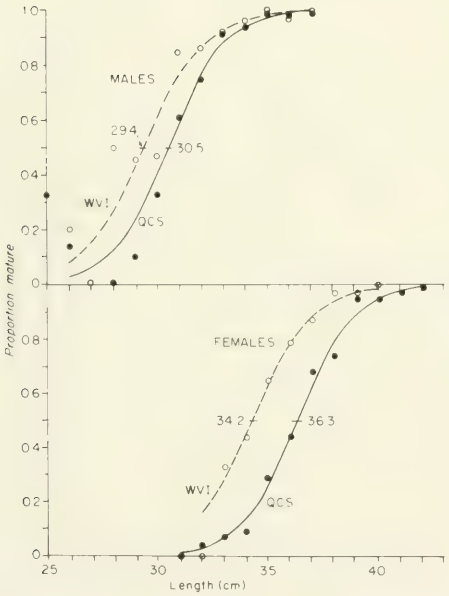

FIGURE 19.—Length-maturity relation for QCS and WVI stocks of Pacific ocean perch, by sex.

ocean perch in the QCS and WVI stocks (Table 14). Predicted curves for proportion mature at each length have been calculated and are represented by the solid lines (QCS stock) and dashed lines (WVI stock) in Figure 19. These curves, and the $l_{0.50}$ estimates they are based on, indicate that both

TABLE 14.—Estimated values of parameters for the equations used to examine length and age at maturity for Pacific ocean perch.

Item	Males		Females	
	QCS stock	WVI stock	QCS stock	WVI stock
	Length at Maturity			
$l_{0.50}$	30.4627	29.3782	36.2705	34.2335
σ	1.2791	1.4170	1.2405	1.3252
Var ($l_{0.50}$)	0.0492	0.0809	0.0105	0.0316
Z statistic[1]	3.0067		9.9277	
	Age at Maturity			
$t_{0.50}$	7.5884	—	11.3775	9.2899
σ	0.9799	—	1.1819	1.6132
Var ($t_{0.50}$)	0.0543	—	0.0204	0.1068
Z statistic[2]	—		5.8533	
$t'_{0.50}$	7.0	6.5	10.3	10.0

[1]For test of between-stock differences in $l_{0.50}$
[2]For test of between-stock differences in $t_{0.50}$.

males and females mature at a much smaller size off Washington and Southwest Vancouver Island than they do in Queen Charlotte Sound.

In order to examine the significance of between-area differences further, the variance of $l_{0.50}$ was approximated by using the delta method:

$$\text{Var}\,(l_{0.50}) = \text{Var}\left(\frac{-\alpha}{\beta}\right) = \frac{1}{\beta^2}\,(\text{Var}\,\alpha) + \frac{\alpha^2}{\beta^4}\,\text{Var}\,(\beta) - 2\,\frac{\alpha}{\beta^3}\,\text{Cov}\,(\alpha, \beta).$$

This variance was estimated for each sex and area considered (Table 14) using information from

the linear regression program previously employed. If it is assumed that the estimates of $l_{0.50}$ are normally distributed, then the quantity

$$\frac{\frac{\alpha_1}{\beta_1} - \frac{\alpha_2}{\beta_2}}{\sqrt{\mathrm{Var}\left(\frac{\alpha_1}{\beta_1}\right) + \mathrm{Var}\left(\frac{\alpha_2}{\beta_2}\right)}}$$

is distributed as Z and can be used to test the hypothesis that there is no difference in $l_{0.50}$ between areas. The Z values obtained for both males and females (Table 14) indicate that the observed differences in length at maturity are highly significant, since $P(Z>3.0067) = 0.0013$ and $P(Z>9.9277) \approx 0$ under the hypothesis being tested.

Age-maturity relation

Age at maturity was estimated by two methods. The first series of estimates was developed by using the logistic equation:

$$P_t = \frac{1}{1 + \exp -\left(\frac{t - t_{0.50}}{\sigma}\right)}$$

where P_t = proportion mature at age t
$t_{0.50}$ = age when $P_t = 0.50$ = age at maturity
σ = constant.

The parameters for this equation were estimated in the same manner described in the length-maturity section, through weighted linear regression analysis of the data in Tables 11-13. The resulting estimates of $t_{0.50}$ and σ are shown in Table 14, and the predicted relationships between P_t and t are shown by the solid lines (QCS stock) and dashed lines (WVI stock) in Figure 20. The $t_{0.50}$ estimates obtained in this way are estimates of the age when males mate for the first time and when females release their first brood of embryos. The Z statistic shows that between-stock differences in age at first brood release were statistically significant, since $P(Z>5.8533) \approx 0$.

A second series of estimates for the age at maturity ($t'_{0.50}$) was obtained by utilizing the $l_{0.50}$ values obtained in the previous section, and von Bertalanffy growth parameters from Table 3. The equation used was:

$$t'_{0.50} = t_0 - \frac{1}{K} \ln\left(1 - \frac{l_{0.50}}{L_\infty}\right)$$

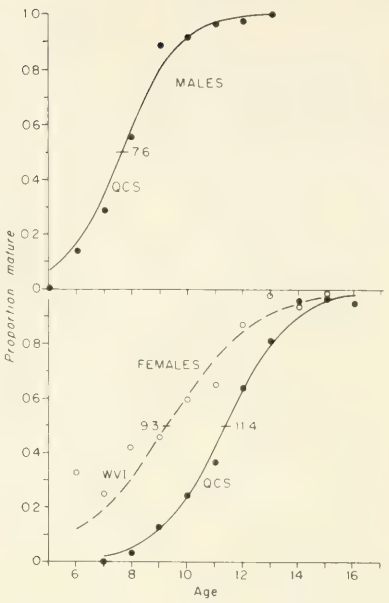

FIGURE 20.—Age-maturity relation for QCS and WVI stocks of Pacific ocean perch, by sex.

Resulting estimates for males (Table 14) are probably quite accurate, since both $l_{0.50}$ and the age-length relations in Table 3 were based on data collected during June-December (near the mating season). The $t'_{0.50}$ estimates for females are biased, however, since a significant amount of growth occurs between the period when $l_{0.50}$ was estimated (February-June) and the period when the age-length data were collected (July for the WVI stock, September-December for the QCS). The bias is relatively small for the WVI stock, but in Queen Charlotte Sound most of the annual growth probably occurs during the intervening time period. The $t'_{0.50}$ value obtained for QCS females consequently underestimates age at first brood release by almost a year.

The results from both methods used to estimate age at maturity (Table 14) indicate that both males and females mature at an earlier age off Washington and southwest Vancouver Island than they do in Queen Charlotte Sound. When biases in $t'_{0.50}$ are considered, it appears that WVI females release their first brood when 9-10 yr old, while those in Queen Charlotte Sound are 11 yr old. Estimates of age at first mating for males were not subject to the same bias as those for females and can be taken directly from Table 14. These results suggest that males first mate at age 6

in the WVI stock and age 7 in Queen Charlotte Sound.

FECUNDITY

Methods Used in Fecundity Determination

Collection of Ovaries

Previous fecundity work on *Sebastes* has indicated that the time of ovary collection must be carefully controlled. Lisovenko (1965) determined fecundity for two groups of Pacific ocean perch in the Gulf of Alaska, the first consisting of 61 fish collected prior to fertilization and the second of 29 fish with fertilized ova. He found that the estimated fecundity of the first group was 1.5-2.0 times higher than that of the second, considering females of comparable size. Lisovenko attributed this difference to eggs bursting when females were hauled to the surface, but accidental extrusion of the fertilized eggs could also have beem implicated. Pacific ocean perch containing fertilized eggs can be made to extrude these eggs by slight pressure on the body cavity and make poor specimens for determination of fecundity.

If ovary samples are collected too far in advance of fertilization, however, maturing oocytes that will be fertilized in the fall are too small to be differentiated from immature oocytes. The optimal time to collect material for fecundity observations is therefore August-November, when immature and maturing oocytes can be differentiated, but fertilization of ova has not yet occurred.

Collection dates and times for fecundity samples used in this study are shown below:

Date (1973)	*Location*	*Number collected*
22 Aug.	Destruction Island, Wash.	14
26 Aug.	Tillamook Head, Oreg.	27
19 Sept.	S.E. Corner, Goose Island	40

All fish from Queen Charlotte Sound were taken from the landings of a commercial trawler, while those from the southern region were collected aboard the U.S.S.R. research trawler *Seskar*. The cruise objectives of the *Seskar* were such that only limited quantities of Pacific ocean perch were caught off Washington, and collections made off the Oregon coast were used to supplement those from the WVI stock.

Since between-area fecundity comparisons were to be made, the attempt was made to collect ovaries from Queen Charlotte Sound when the fish were in the same stage of the reproductive cycle as those off Washington and Oregon. Despite this, gross examination of male gonads and data on oocyte diameters (Gunderson 1976) indicated that fish in the Queen Charlotte Sound collection were not quite as advanced as those collected 1 mo earlier off Washington and Oregon.

All ovaries collected were placed in modified Gilson's solution (Bagenal and Braum 1968) to harden the eggs and separate them from surrounding ovarian tissue. After about 1 mo, ovarian tissue was removed from the eggs and the fluid was changed. After the samples had been in Gilson's solution for a total of 3 mo, they were removed and stored permanently in 10% ethyl alcohol.

Differentiation of Mature and Immature Oocytes

A series of ovaries was collected over the whole range of the reproductive cycle so that the growth progression of maturing oocytes could be followed. All specimens were collected in the Washington-Oregon region and their ovaries were placed in Gilson's solution until the oocytes separated from ovarian tissue. Subsampling of the eggs in an ovary was accomplished by the same technique used to estimate fecundity (described below).

The size frequency for the eggs in a specimen was obtained by systematically measuring (nearest 0.01 mm) those eggs lying on transect lines drawn on a Petri dish, until a desired sample size had been attained. Many of the eggs were elliptical or irregularly shaped and, in these cases, the longest axis parallel to the counting scale was selected for measurement. One specimen was in the "embryo or eyed larvae" stage of maturity and, in this particular instance, all eggs with embryos were measured along the longitudinal axis of the embryo.

The results (Figure 21) showed that there was a significant overlap in the size of immature and maturing oocytes during the period when fecundity samples were collected. By October, the size of maturing oocytes had increased substantially and differentiation of maturing oocytes was straightforward. Following fertilization of the first brood, however, it appears that other groups of oocytes begin to mature, so that several sizes of eggs and embryos are present in ovaries that have

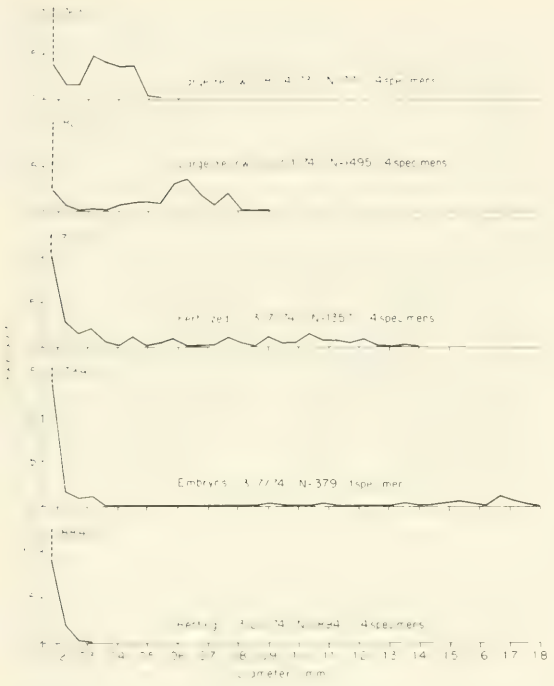

FIGURE 21.—Size composition of oocytes, ova, and larvae within Pacific ocean perch ovaries at different stages of the reproductive cycle. Maturity stage of the gonads these data were collected from is shown above each size frequency curve. Numbers in parentheses indicate the percentage of oocytes that are 0.15 mm or smaller.

passed the fertilization stage. There was no single dominant mode of mature eggs or larvae in any of the fertilized specimens that were examined (Table 15).

Despite the wide range of egg size and development within fertilized specimens, most of their progeny will probably hatch and be released at about the same time. Field observations (Gunderson 1974) indicate that most embryos are released during a single spawning peak that lasts only 2 or 3 wk.

TABLE 15.—Oocyte size frequencies for individual specimens of "fertilized" Pacific ocean perch females.

Oocyte size class (mm)	Number observed				Oocyte size class (mm)	Number observed			
0.159	262	237	240	227	0.789-0.833	4	1	—	—
0.159-0.203	30	30	26	54	0.834-0.878	—	1	—	—
0.204-0.248	13	10	7	10	0.879-0.923	11	2	1	2
0.249-0.293	5	6	4	7	0.924-0.968	4	—	2	—
0.294-0.338	19	5	3	1	0.969-1.013	4	2	1	—
0.339-0.383	6	1	1	—	1.014-1.058	2	4	10	3
0.384-0.428	1	1	—	—	1.059-1.103	2	4	4	—
0.429-0.473	7	2	1	6	1.104-1.148	1	2	5	1
0.474-0.518	1	—	—	1	1.149-1.193	—	2	2	2
0.519-0.563	3	—	—	2	1.194-1.238	—	5	6	—
0.564-0.608	1	2	2	7	1.239-1.283	—	—	1	—
0.609-0.653	—	—	—	1	1.284-1.328	—	—	—	—
0.654-0.698	2	—	—	—	1.329-1.373	—	2	1	—
0.699-0.743	2	1	—	—	Total	395	321	317	324
0.744-0.788	15	1	—	—					

In view of the oocyte measurement results and the fact that studies on the fecundity of *Sebastes marinus* have suggested a strong element of failure in oocyte fertilization (Raitt and Hall 1967), it seems that current estimates of fecundity must be regarded as somewhat tentative. Complex changes in fecundity probably occur after the first brood of oocytes has been fertilized and detailed morphological work will be required to determine their significance.

For purposes of this study, fecundity was estimated from the number of mature oocytes present prior to fertilization. All oocytes less than 0.30 mm in diameter were classified as immature on the basis of preliminary comparisons of oocyte size frequencies for juvenile and adult specimens. The data in Figure 21 suggest that this cutoff point was somewhat high, however, and that many of the oocytes in the 0.25- to 0.30-mm size class eventually mature. Even if all oocytes that were in the 0.249- to 0.293-mm size class during the collection period were actually maturing, the error generated by calling them immature would be less than about 10%.

Counting the Oocytes

Fecundity was estimated through subsampling by volume. The ovarian contents from each fish were removed from the storage solution, passed through a 1.17-mm screen to remove large particles of ovarian tissue that remained, and placed in a large beaker; water was then added until 2,000 ml of oocytes and water had been obtained. The mixture was stirred magnetically until all oocytes were distributed throughout the water column and a 5-ml subsample withdrawn with a pipette. Care was taken to sample all parts of the water column with the pipette. Four to six subsamples were taken in this manner, the exact number depending on the standard deviation of the first four subsamples.

The oocytes in each subsample were then counted, using a binocular microscope. Two or three replicate counts of each subsample were made by two different observers during the early phases of the study. The number of replicate counts was gradually reduced, however, as it became clear that there was little variation between them. Throughout the study, all counts for a given

fish were partitioned between two different observers to balance out the effects of any bias.

The mean number of eggs per milliliter was calculated for each of the 4-6 subsample means from a given specimen and the coefficient of variation (CV = standard deviation/mean of subsample counts) for these subsample means had the following distribution:

Range of CV *(%)*	*Washington-Oregon*	*QCS*	*Total*
0.0- 4.9	5	4	9
5.0- 9.9	10	16	26
10.0-14.9	17	12	29
15.0-19.9	4	7	11
20.0-24.9	3	1	4
Total	39	40	79

For most specimens (81%), the standard deviation of the subsample means was within 15% of the grand mean. The fecundity of each specimen was estimated by using the formula: $F = 2{,}000n$, where F = fecundity and n = mean number of eggs per milliliter in the subsamples.

Results of Fecundity Study

May (1967) reviewed the results of fecundity work on several species (cod, *Gadus morhua;* herring, *Clupea harengus pallasi;* long rough dab, *Hippoglossoides platessoides*), which showed that, for most practical purposes, variation in fecundity is adequately explained in terms of length alone. Raitt and Hall (1967) came to the same conclusion in their work on the Atlantic redfish, *Sebastes marinus,* a species belonging to the same genus as Pacific ocean perch. They carried out multiple regression of $\log F$ and $\log L$ using weight or age as second independent variables, and it was found that inclusion of variates other than length did not significantly reduce residual variation. As a result, the fecundity work in the current study was directed primarily toward determining the relation between fecundity and length.

Fecundity data for *Sebastes alutus* seemed to fit the relation $F = aL^b$, where F = number of oocytes in thousands, L = fork length in centimeters, and a and b = constants.

The values of a and b were determined by transforming this equation into: $\log F = \log a + b \log L$ and using linear regression techniques to fit $\log F - \log L$ data to a straight line. Data from Washington-Oregon and Queen Charlotte Sound were treated separately, and the following results were obtained:

Washington-Oregon

$$F = (0.19295 \times 10^{-9}) L^{7.32506}$$

Queen Charlotte Sound

$$F = (0.12240 \times 10^{-6}) L^{5.51258}$$

Predicted fecundity at each length was calculated from these relationships, and is shown in Figure 22. The significance of between-area differences in the length-fecundity relation was examined statistically, using the BMD 3R4V[4] computer program for analysis of covariance. The results of this analysis showed that between-area differences in the fecundity-length relation are statistically significant at the 95% level and that they are due to differences in the intercepts of the $\log F - \log L$ regression lines ($F = 5.85$ with 1,76 df) rather than to differences in their slope ($F = 3.43$ with 1,75 df).

Two workers (Westrheim 1958; Snytko 1971) have previously examined the length-fecundity relation for Pacific ocean perch off Washington-Oregon, although neither carried out corresponding studies for the Queen Charlotte Sound stock. Westrheim's results were the first available and were based on examination of 13 specimens. Westrheim collected his fecundity samples during September-November (1951 and 1952), estimated

[4]BMD 3RV. Regression with Analysis of Covariance. This is an addition to the University of California BMD program series, developed at the University of Washington Computer Center by W. Farr.

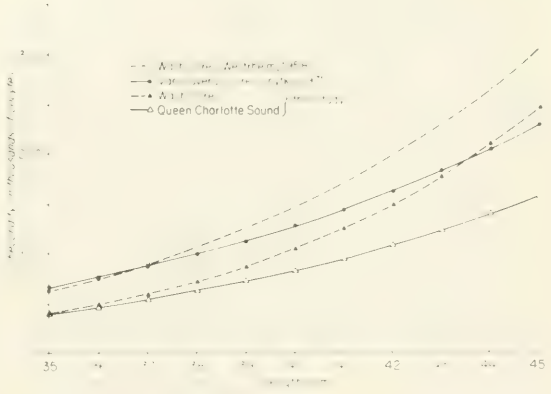

FIGURE 22.—Relation between fecundity and length for Pacific ocean perch off Washington-Oregon (as determined by three different workers) and in Queen Charlotte Sound.

fecundity by a gravimetric method, and found that his results could be represented by the relation: $F = (4.8556 \times 10^{-15})L^{6.33454}$, where L = fork length in millimeters.

Snytko's (1971) fecundity observations on 171 specimens were the most extensive made to date in the Washington-Oregon region. Snytko collected his fecundity samples during November-March 1967-68, in the "Vancouver-Oregon region" (lat. 40°-50°N). The ovaries were collected before fertilization of the oocytes had occurred and fecundity was determined gravimetrically by counting the oocytes present in 0.5- to 1.0-g subsamples of the ovaries (Snytko and Borets 1972). Snytko (1971) presented his data in terms of mean fecundity at a given length and regression of $\log F$ on $\log L$ indicates that they can be represented by the relation: $F = (0.13103 \times 10^{-5})L^{4.98838}$, where L = length in centimeters.

Length-fecundity relationships for Pacific ocean perch off Washington-Oregon, as predicted by Westrheim (1958), Snytko (1971), and myself are shown in Figure 22. There was substantial variation in the results obtained by different workers and this is to be expected in view of the differences in the timing of ovary collection, techniques used to subsample and count oocytes, and the wide expanse of time (1951-73) covered by the studies. There is also a strong possibility that length-fecundity differences exist between substocks within the Washington-Oregon region and could have contributed to these differences.

The variability in the results of different workers reflects only the difficulties in estimating the number of maturing oocytes a given fish will produce and leaves a larger question unanswered. What we would really like to estimate is the number of viable larvae that fish of a given length or age will give birth to during the embryo-release period, and yet we are totally ignorant of the relationship between the estimated number of maturing oocytes and the number of larvae that will result from them.

Preliminary estimates of the number of larvae that will be released at each age can be made, however, if it is assumed that all oocytes present immediately after fertilization will develop into viable larvae. It should be kept in mind that even though this assumption is patently false, the resulting estimates are still well-suited to between-area comparisons if oocyte-larval mortality does not differ between areas.

It will be recalled that fecundity observations applied to fish collected during August-September, while estimates of mean length at each age applied to the September-December period for Queen Charlotte Sound and to July in the case of the WVI stock. The estimate of the number of larvae released during March of any given year of life (Table 17) was consequently obtained by combining the age-length and length-fecundity relationships pertaining to the previous July-December. For example, the estimated number of larvae released by 11-yr-olds in Queen Charlotte Sound was estimated from predicted mean length at age 10 (Table 3), and the length-fecundity relationship appropriate to that stock ($F = 0.12240 \times 10^{-6} L^{5.51258}$).

RESPONSE OF PACIFIC OCEAN PERCH STOCKS TO FISHING

Methods Used to Examine the Effects of Fishing

In the past, management recommendations for Pacific ocean perch in the INPFC Vancouver area have been developed by arriving at some estimate of the fishing mortality (F) that the stock can withstand, then applying this value to the best available estimate of stock biomass to arrive at a quota. Much discussion has consequently focused on what levels of F can be sustained.

In this section, the effects of different levels of fishing intensity on a hypothetical cohort of fish will be examined, with an approach similar to the yield per recruit analysis that is commonly used in stock assessment. In contrast to conventional yield per recruit analysis, however, I have attempted to look at the costs involved in exerting high levels of fishing intensity on a population, as well as the benefits of increased yield. In particular, the decline in exploitable biomass (CPUE/q, where q is the catchability coefficient) and population fecundity that go hand in hand with increases in yield have been evaluated quantitatively.

The basic computations used to accomplish this are shown in Table 16. Data required included age-specific schedules of instantaneous natural mortality, vulnerability to fishing, mean weight, and fecundity (Table 17). The mean weight schedule represents average values for the entire year, while the fecundity schedule applies to the embryo release period at the beginning of the year. Vulnerability and mortality were assumed to be constant throughout the year.

TABLE 16.—Example of computations used to estimate exploitable biomass, yield, and population fecundity for a hypothetical Pacific ocean perch population based on N_0 recruits. Input parameters needed are indicated by asterisks.

Age	M_i* Natural mortality coefficient	V_i* Vulnerability coefficient	s_i Proportion alive at beginning of age i	N_i Number alive at beginning of age i	W_i* Mean weight	B_i Mean biomass	B_i Mean exploitable biomass	Y_i Yield	m_i* Fecundity	E_i Population fecundity
0 t_p	M_0	V_0	s_0 1	$N_0 s_0$ (N_0)	W_0	$\frac{N_0 W_0}{V_0 F + M_0}[1 - \exp(V_0 F + M_0)]$	$V_0 B_0$	$FV_0 B_0$	m_0	$N_0 m_0$
1	M_1	V_1	s_1 $\exp(V_0 F + M_0)$	$N_0 s_1$	W_1	$\frac{N_1 W_1}{V_1 F + M_1}[1 - \exp(V_1 F + M_1)]$	$V_1 B_1$	$FV_1 B_1$	m_1	$N_1 m_1$
2	M_2	V_2	s_2 $s_1 \exp(V_1 F + M_1)$	$N_0 s_2$	W_2	$\frac{N_2 W_2}{V_2 F + M_2}[1 - \exp(V_2 F + M_2)]$	$V_2 B_2$	$FV_2 B_2$	m_2	$N_2 m_2$
3	M_3	V_3	s_3 $s_2 \exp(V_2 F + M_2)$	$N_0 s_3$	W_3	$\frac{N_3 W_3}{V_3 F + M_3}[1 - \exp(V_3 F + M_3)]$	$V_3 B_3$	$FV_3 B_3$	m_3	$N_3 m_3$
							$\sum V_i B_i$ B	$\sum Y_i$ Y		$\sum E_i$ E

TABLE 17.—Vital statistics for females from the QCS and WVI stocks of Pacific ocean perch.

Age	Mean length (cm)	Mean weight[1] (g)	Fecundity (thousands)	Proportion vulnerable to fishing[2]
		WVI Stock		
8	31.4	433	12.1	0.10
9	32.9	502	17.8	0.20
10	34.3	573	25.1	0.35
11	35.5	639	34.0	0.52
12	36.6	704	43.7	0.64
13	37.6	766	54.7	0.69
14	38.6	833	66.6	0.75
15	39.4	889	80.8	0.87
16	40.2	947	93.9	1.00
17	41.0	1,008	108.8	1.00
18	41.6	1,056	125.7	1.00
19	42.2	1,105	139.8	1.00
20	42.7	1,147	155.2	1.00
21	43.2	1,190	169.2	1.00
22	43.7	1,234	184.3	1.00
23	44.1	1,270	200.5	1.00
24	44.5	1,307	214.3	1.00
		QCS Stock		
9	34.3	573	—	0.20
10	35.9	662	—	0.31
11	37.2	741	45.7	0.44
12	38.5	826	55.7	0.53
13	39.6	903	67.3	0.62
14	40.6	977	78.6	0.79
15	41.4	1,040	90.1	0.94
16	42.2	1,105	100.4	1.00
17	42.9	1,164	111.5	1.00
18	43.6	1,225	122.1	1.00
19	44.1	1,270	133.5	1.00
20	44.6	1,316	142.2	1.00
21	45.0	1,354	151.3	1.00
22	45.4	1,392	158.9	1.00
23	45.8	1,431	166.9	1.00
24	46.1	1,461	175.2	1.00

[1]Estimated from the age-length data in Table 3 and Westrheim and Thomson's (1971) all-B.C. length-weight relation for females: $W = 0.0078571 L^{3.16734}$

[2]Vulnerability coefficients for 8- and 9-yr-olds were assigned arbitrarily. The values used were more conservative than those predicted by extrapolation of the straight line obtained for 10- to 16-yr-olds (0.20 for 8-yr-olds and 0.29 for 9-yr-olds).

Yield, exploitable biomass, and total fecundity are calculated for each age group, then summed. The results give the annual yield to the fishery, annual production of larvae, and average exploitable biomass on hand during the year for an equilibrium population of Pacific ocean perch. This population is based on a constant number of recruits (N_0), with individual growth and mortality being determined by the input values of the constants used to describe mortality, vulnerability to fishing, and mean weight at each age.

A computer program[5] was written to carry out the calculations in Table 16 and offers a variety of ways to evaluate the effects of different fishing strategies on a stock. The basic calculations can be carried out for any combination of instantaneous rates of fishing mortality (F) and age of entry into the fishery (t'_p) that the user specifies.

The mesh size used when fishing for Pacific ocean perch is dictated primarily by convenience, since the incidence of "gilling" and entanglement in the meshes is reduced sharply when using 3.0-inch mesh (internal measure) in the cod end. This was not found to be the case in mesh studies with Atlantic redfish (Templeman 1963), where use of smaller cod end mesh sizes simply "gilled" fish of a smaller size. In the Pacific ocean perch stocks examined in this paper, recruitment to the fishing grounds is quite gradual and the fish that would normally be "gilled" in a 3.0-inch cod end are poorly represented on the grounds.

Pacific ocean perch offer a special case then, where evaluation of the effects of different size or age restrictions is of no practical interest for fisheries management. Consequently, all analysis in this section was focused on determining the optimal intensity of fishing for the Pacific ocean

[5]D. Gunderson and J. Buss. 1976. Users guide to ASSESS: Assessment of the effects of different fishing strategies on fish populations (FORTRAN IV). Norfish Pap. NC09, 8 p.

perch stocks being examined and the effects of varying the age at entry into the fishery (t'_p) were ignored.

In addition, the analysis was restricted to the female portion of the stock. Over the long term, the population will be far more sensitive to removals of females and reduced population fecundity than it will to removals of males, and the optimal harvest rate for females will determine the level of F that should be applied to the stock as a whole.

The input data used to describe the QCS and WVI stocks are shown in Table 17. The values used for mean weight at age, vulnerability coefficients, and fecundity at age were derived from the information in Tables 3 and 6 and Figure 22. Natural mortality was assumed to be the same for all age groups concerned and computations were carried out for both $M = 0.1$ and $M = 0.2$.

Assessment of Immediate Response to Fishing

Only a small fraction of fish less than 8 yr old are recruited to the fishing grounds and, for the purposes of this study, it was assumed that recruitment begins at age 9 ($t_p = 9$). It is possible that significant quantities of 9-yr-olds are discarded by fishermen, however, making it difficult to estimate their vulnerability coefficient from market samples. For this reason, $t_p = 10$ was also considered, so that the sensitivity of the results to changes in t_p could be evaluated.

The results (Figure 23) showed that different values of t_p had very little effect on the relative trends in yield, population fecundity, and exploitable biomass with increasing F. In fact, the relative levels of each followed almost identical trends for both stocks and both values of t_p considered. However, the value of M used in the calculations had a pronounced effect on the results.

In all cases examined, there was a sharp rise in yield as F increased from 0.0 to 0.2, and a more gradual increase for F-values greater than 0.2. Relative levels of exploitable biomass and population fecundity showed a reciprocal trend, decreasing sharply as F increased from 0.0 to 0.2, then declining more gradually for F greater than 0.2.

Relative changes in population fecundity were almost identical to changes in exploitable biomass, indicating that changes in CPUE can be used directly to estimate the magnitude of changes in population fecundity. During 1966-68, then, population fecundity for stocks in the Oregon-Queen Charlotte Sound region must have declined in the same manner as CPUE and is currently only about 50% of what it was prior to intensive fishing.

Preliminary examination of the data (Figure 23) shows that the most significant changes in yield, exploitable biomass, and population fecun-

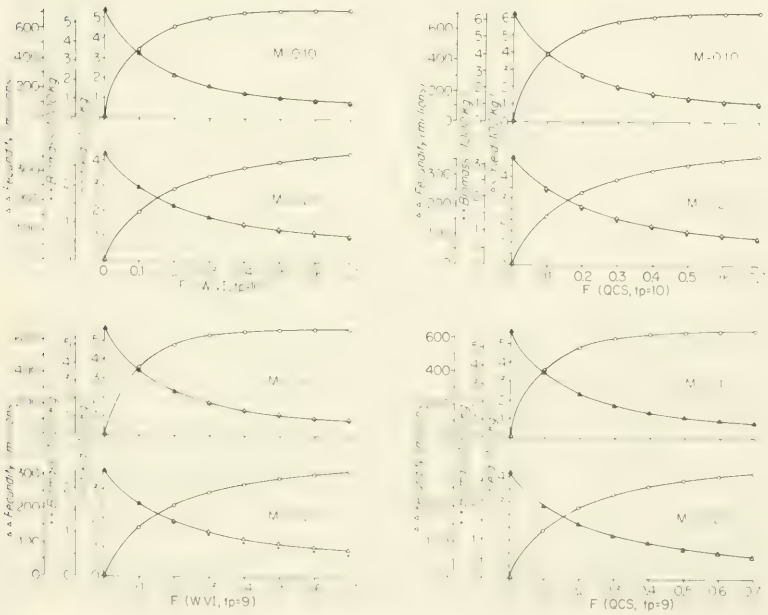

FIGURE 23.—Population fecundity (estimated number of larvae released annually), exploitable biomass, and annual yield for hypothetical populations based on 1,000 recruits per year. Results are presented by stock, for two different ages at recruitment (t_p) and two different levels of instantaneous natural mortality (M).

TABLE 18.—Relative yield (Y/Y_{max}), population fecundity (E/E_{max}), and exploitable biomass (B'/B'_{max}) at $F = 0.1$ and 0.2.[1] The range of values obtained by taking $t_p = 9$ or 10, for two different stocks of Pacific ocean perch is presented.

Item	$F = 0.1$		$F = 0.2$	
	$M = 0.1$	$M = 0.2$	$M = 0.1$	$M = 0.2$
Y/Y_{max}	0.62-0.64	0.45	0.84-0.85	0.67
E/E_{max}	0.59-0.62	0.68-0.70	0.40-0.43	0.51-0.53
B'/B'_{max}	0.60-0.61	0.68	0.40-0.41	0.50-0.51

[1] Y_{max} = yield when $F = 0.7$; E_{max} and B'_{max} = population fecundity and exploitable biomass when $F = 0.0$.

dity occurred when $F = 0.1$ and $F = 0.2$, and the results for these two levels of fishing intensity have been summarized in Table 18. All data were presented in terms of the range of values obtained when considering different stocks and t_p values. The ranges were always quite narrow, attesting to the fact that consideration of different stocks and t_p values had little influence on the results.

The conclusions that can be drawn from Table 18 depend to a large degree on what is considered to be the best estimate of M. If $M = 0.1$, the costs of letting F reach 0.2 are quite high, since exploitable biomass and population fecundity would be reduced to about 40% of their virgin stock levels. From this consideration alone, it would seem advisable to limit F to 0.1.

If $M = 0.2$, however, the costs of letting F reach 0.2 are somewhat lower with exploitable biomass and population fecundity declining to about 50% of their level in the virgin stock. Limiting F to 0.1 would reduce the yield to only 45% of the level attainable at $F = 0.7$, while population fecundity and exploitable biomass would undergo reductions of about 30% from virgin stock levels.

On the basis of this analysis, then, there is a reasonable possibility that if $M = 0.2$, the optimal level of F could be as high as 0.2. From a biological point of view, however, a central question still remains unanswered, since we have not yet evaluated the consequences of reducing population fecundity. It is one thing to point out the degree to which population fecundity will be reduced by various levels of fishing intensity and quite another to determine the impact this reduction will have on future recruitment.

Effects of Fishing on Future Recruitment

Variability in egg and larval survival is extremely high for marine teleosts. Larvae grow rapidly during the planktonic phase and require large quantities of food. For example, haddock larvae initially grow at rates of about 12% per day, increasing in weight by a factor of 10^5 during their first year of life (Jones 1973). When food is not plentiful, available supplies can be exhausted rapidly, resulting in starvation and high rates of density-dependent mortality. Even if larval mortality is not directly due to starvation, density-dependent mortality could easily result from slow growth and prolonged exposure to predators (Cushing 1974).

Density-independent mortality, such as that suffered when eggs or larvae are swept into unfavorable nursery areas, can also be quite variable. Ketchen (1956) and Ketchen and Forrester (1966) found that in the case of English sole and petrale sole, mortality of this nature seems to account for a high proportion of the variability in year class strength.

Marine fish have evolved three basic ways of adapting their life history to cope with the highly variable survival of their progeny: 1) iteroparity (repeat spawning), 2) high fecundity, and 3) complete elimination of the egg and/or larval stage through ovoviviparity or viviparity. Murphy (1968) has shown that iteroparity is favored under conditions of high variability in larval survival and relatively constant adult mortality. This line of evolution leads to the existence of a large number of adult age-groups—a common situation in marine fishes. With several adult age-groups in the population, the size of the adult stock is buffered somewhat against variations in the strength of individual year classes.

High fecundity and elimination of the planktonic phase offer two divergent means of coping with variable larval mortality and are typified best by the gadoids on one hand and by elasmobranchs on the other. Atlantic cod commonly produce several million eggs per adult, and Cushing and Harris (1973) have shown that the spawner-recruit relation for this species is distinctly convex or dome-shaped (curve a in Figure 24). This relationship implies that eggs are "overproduced" at high parental stock densities, with attendant declines in larval survival. At stock densities below the replacement point (P_r), the high fecundity allows for great resilience and rapid return to P_r.

The development of most elasmobranchs is characterized by the elimination of the larval stage found in the majority of teleosts and the young are fully developed when born. Fecundity is extremely low, with 2-108 young being produced

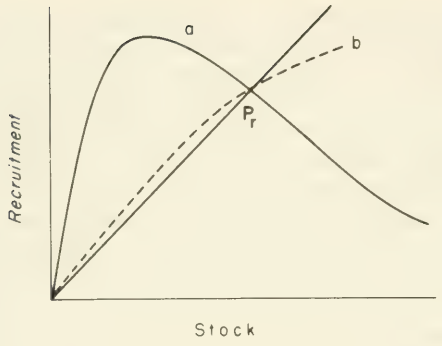

FIGURE 24.—Relationship between parent stock and recruitment for gadoids (a) and elasmobranchs (b).

per year (Holden 1973). Any compensatory responses to increase the number of recruits must act through changes in growth (with attendant changes in the age at maturity) or fecundity, and are relatively sluggish. Holden (1973) has suggested that the stock-recruitment relation for most elasmobranchs is probably of the form of curve b in Figure 24, departing little from the bisector on either side of the replacement point.

By eliminating the free-living larval stage, elasmobranchs have reduced the susceptibility of adult stock size to environmental perturbations. In the natural state, then, the compensatory mechanisms that return the stock to P_r do not need to provide the same degree of resilience they do in the gadoids. This lack of resilience makes the elasmobranchs poorly adapted to harvests by man, however, and they are quite susceptible to overfishing.

Pacific ocean perch are ovoviviparous, and, like the elasmobranchs, they are probably much less resilient to perturbations from P_r than a highly fecund, oviparous species like cod. It is important, therefore, that population fecundity be kept quite near the levels found in the virgin stock when the adult stock was presumably near P_r. Any reduction in population fecundity from virgin stock levels could easily result in reduced recruitment.

Some increases in the number of larvae released could probably come through compensatory growth, since the age at sexual maturity and level of individual fecundity are both correlated strongly with size. There must be some limits to the degree of compensation this mechanism is capable of, however, and this was explored quantitatively by using the model (Table 16) and computer program described previously.

This analysis was begun by setting up four sets of hypothetical populations (one set for each stock) and calculating the population fecundity under different levels of fishing mortality. In the first population, the "standard" age-length data in Table 17 were used to describe individual growth in each stock. In the second and third populations, the mean lengths at each age were increased 3% and 5% (Figure 25) to simulate compensatory growth. In the fourth population, mean length at each age was again increased 5% above standard, and it was also assumed that sexual maturation occurred 1 yr earlier than in the other populations. The latter assumption was justified by the fact that a 5% increase in growth brought 8-yr-olds from the WVI stock and 10-yr-olds from the QCS stock up to the size at which sexual maturity occurred in the standard population (Figure 25). The last population was presumed to embody the maximum possible degree of compensation in population fecundity, since the projected increases in mean length at age would be quite remarkable in a species growing as slowly as *S. alutus*. The assumption that the age at sexual maturity would decline because of earlier attainment of a critical maturation size is also tenuous, and only time will tell if this actually occurs.

The age of recruitment was taken as age 8 for the WVI stocks and age 10 for the QCS stocks, in

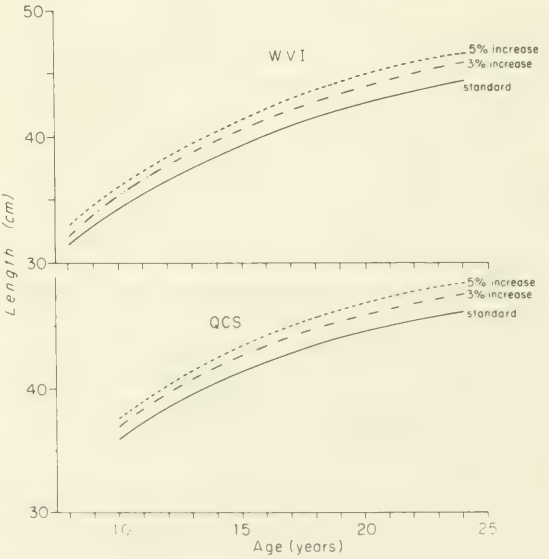

FIGURE 25.—Mean length at age for female Pacific ocean perch in the WVI and QCS stocks, assuming standard growth, and two different levels of compensatory increase in growth.

TABLE 19.—Estimated population fecundity (millions of larvae released) for hypothetical Pacific ocean perch populations based on 1,000 recruits per year, under different levels of fishing mortality and compensatory growth and maturity.

Item	WVI stock F 0.0	0.1	0.2	Item	QCS stock F 0.0	0.1	0.2
			M = 0.1				
Standard growth, mature at age 9	607	356	237	Standard growth, mature at age 11	703	437	302
3% increase, mature at age 9	753	442	294	3% increase, mature at age 11	828	515	356
5% increase, mature at age 9	867	510	339	5% increase, mature at age 11	920	572	396
5% increase, mature at age 8	884	527	357	5% increase, mature at age 10	966	618	442
			M 0.2				
Standard growth, mature at age 9	256	174	130	Standard growth, mature at age 11	358	251	191
3% increase, mature at age 9	318	216	162	3% increase, mature at age 11	422	296	225
5% increase, mature at age 9	366	249	187	5% increase, mature at age 11	469	328	249
5% increase, mature at age 8	383	266	204	5% increase, mature at age 10	515	375	296

order to accommodate the changes in age at maturity. It was assumed that the length-weight relationships, length-fecundity relationships, and vulnerability coefficients characterizing the standard populations would apply to the other populations as well. All calculations have been carried out for $M = 0.1$ and $M = 0.2$.

The results (Table 19) for standard growth when $F = 0$ give the estimated population fecundity for the virgin stock. In actual fact, biomass was reduced below virgin stock levels several years prior to the time when the "standard" rates of growth were estimated and some compensatory changes could already have occurred. The population fecundity in the "standard" population when $F = 0$ could consequently overestimate preexploitation fecundity to some degree.

For both stocks considered, fishing mortalties greater than $F = 0.1$ doom Pacific ocean perch to lower levels of population fecundity than those existing prior to exploitation. None of the populations examined were able to recover preexploitation levels of population fecundity when $F = 0.2$, even when mean length at age increased by 5% and sexual maturation occurred a year earlier than normal.

Even if F is restricted to 0.1, the ability to regain virgin stock levels of fecundity varies sharply with M. If $F = M = 0.1$, the results for both stocks show that even if growth increases by 5% and sexual maturation occurs a year earlier than normal, population fecundity will be 12-13% less than in the virgin stock. If $M = 0.2$, the outlook is better, since the stocks were able to recover 92-97% of the preexploitation fecundity with a 5% increase in growth.

The main point to be considered, however, is that even when $F = 0.1$, Pacific ocean perch would have to undergo significant compensatory changes in growth to regain virgin stock levels of population fecundity and would possibly have to mature a full year earlier than normal. In this light, the intensive fishing of the U.S.S.R. and Japanese trawl fleets in the past has been quite remote from the concept of long-term equilibrium yield.

In the case of the WVI stock, exploitation was most intensive during 1967, and, depending on the value of M used, 1967-68 estimates of F ($= Z - M$) would range from 0.36 to 0.46 (Figure 17). In almost every year since, the estimated value of F would exceed 0.1, regardless of whether $M = 0.1$ or 0.2. The situation is less clear in the case of the QCS stock, but mortality estimates based on the age composition of the Washington trawl fleet (Figure 16) indicate that F was between 0.66 and 0.76 during 1968-69 and exceeded 0.1 during 1969-72.

Drastic action will probably be required to return Pacific ocean perch to their former levels of population fecundity, beginning perhaps with a total ban on commercial fishing, such as that proposed by Snytko (1971). Once this has been accomplished, harvest from both the QCS and WVI stocks should be regulated so that the catch does not exceed 0.1 $\hat{\beta}$, where $\hat{\beta}$ is the estimated stock biomass.

SUMMARY

Pacific ocean perch are a dominant component of the fauna of the North Pacific, attaining a wide geographic distribution and high levels of population density prior to exploitation. Intensive exploitation by man created a sudden change in their population biology, and one that they were poorly adapted to cope with. Pacific ocean perch stocks lack the resilience of highly fecund, oviparous groups like the gadoids and their ability to main-

tain even current levels of abundance is uncertain.

The biology and population dynamics of Pacific ocean perch in the Washington-Queen Charlotte Sound region were examined in detail, to gain some insight into the effects of different fishing strategies on this species. Two stocks were delineated: one in Queen Charlotte Sound (QCS stock) and one inhabiting the waters off northern Washington and southern Vancouver Island (WVI stock).

Production in the region occupied by the WVI stock plummeted from 39,000 metric tons in 1967 to 6,000 metric tons in 1969 (an 85% decline), and catch per hour by North American trawlers declined 45% during the same period. The QCS stock was affected less drastically by fishing, since biomass estimates and CPUE data indicated that *S. alutus* were initially more abundant in the former area and did not undergo such intensive exploitation. During 1966-68, production declined 50%, while CPUE of Washington trawlers declined 36%.

Changes in size and age composition of Pacific ocean perch in the commercial landings were examined for the years 1967-73. Substantial quantities of large *S. alutus* were present in Queen Charlotte Sound during 1956-58 and subsequent changes in size and age composition reflected the changes caused by commercial fishing and recruitment of two strong series of year classes. The first series was centered around the 1952 year class and included the 1951-53 brood years, while the second series centered around the 1961 and 1962 brood years. Size composition data for the WVI stock were too limited to be useful prior to 1961, but data for subsequent years suggested that the same year classes that predominated in Queen Charlotte Sound were also predominant in landings from the WVI stock.

Fisheries exploitation has resulted in drastic reductions in the abundance of the 1951-53 year class series in both the QCS and WVI stocks and the 1973 Washington trawl catches from these stocks were dominated by 10- to 13-yr-old fish.

Growth rates were estimated from commercial fisheries and research cruise data, taking pertinent features of the life history such as seasonal and bathymetric variability in the age-length relation into consideration. Parameters of the von Bertalanffy growth model were estimated by sex for both the QCS and WVI stocks.

Although fish older than age 10 are large enough that almost all can be caught by conventional trawling gear and retained for market sales, age composition data from commercial catches and research surveys showed that recruitment to the fishing grounds is not complete until much later than age 10. The proportion of each age group vulnerable to fishing (V_i) was estimated by employing a model that assumed that natural mortality (M) and V_i were constant throughout the year. The results suggested that recruitment to the fishing grounds differed somewhat between stocks, but that V_i ranged from 0.31-0.35 during age 10 to 0.87-0.94 during age 15. Estimation of V_i could not be made for fish less than 10 yr old, since these age groups may be subject to substantial rates of discard by fishermen.

Any yield per recruit analysis of Pacific ocean perch stocks must take these recruitment patterns into consideration to be meaningful. Recruitment to the fishing grounds is quite gradual, and many age groups that could potentially be retained by conventional mesh sizes are poorly represented on the fishing grounds. Evaluation of the effects of different size or age restrictions would be quite misleading if this were not considered.

Age composition data (number caught per hour by age-group) were used to estimate the survival of 14- to 18-yr-old Pacific ocean perch in year n to ages 15-19 in year $n + 1$, or to ages 16-20 in year $n + 2$. These survival estimates were then converted to total instantaneous mortality rates (Z) and plotted against total international effort ($\bar{f}$) on the assumption that they conform to the model: $Z = q\bar{f} + M$, where M = instantaneous natural mortality rate. The data seemed to fit this model in a general way but there was a relatively low correlation between Z and $\bar{f}$ (r = 0.3-0.5), due principally to wide variability in the availability of Pacific ocean perch to on-bottom trawls (totally unrelated to variations in actual abundance) and to the low quality of the data on international fishing effort. Despite this, there was good agreement between the estimates of M derived from this study (0.07 for the QCS stock and 0.23 for the WVI stock) and results obtained in previous studies. It was concluded that between-stock differences in natural mortality probably should not be overemphasized, and that the results of the mortality studies served mainly to show that M in the Washington-Queen Charlotte Sound region lies in the range between 0.1 and 0.2.

Data on the proportion of sexually mature individuals in each age-length group were sum-

marized by stock and suggested that maturation of both male and female Pacific ocean perch depends more on the size of a fish than on its age. The maturation length (where 50% of the fish in that length group are sexually mature) showed statistically significant differences between stocks, fish from the WVI stock maturing at a smaller size than those from the QCS stock. Males matured at 29.4 cm in the WVI stock and 30.5 cm in the QCS stock, while corresponding values for females were 34.2 and 36.3 cm.

Estimates of the age at sexual maturation indicated that WVI females release their first brood when 9-10 yr old, while those in Queen Charlotte Sound are 11 yr old. The results for males suggest that males from the WVI stock mate for the first time when 6 yr old, while this occurs at age 7 in the QCS stock.

Measurement of oocyte diameters from a series of ovaries collected over the complete extent of the reproductive cycle suggested that any estimates of fecundity must be regarded as tentative, owing to the uncertain significance of auxiliary modes of oocytes. Incomplete fertilization of oocytes also complicates the situation, and there is very little known about the relation between the number of developing oocytes and the number of viable larvae that will result from them.

Length (L)-fecundity (F) data were summarized by stock and were described by the relation: $F = aL^b$. Analysis of covariance showed that there were significant between-area differences in the length-fecundity relationship, females from Washington-Oregon being more fecund than Queen Charlotte Sound females of comparable length.

The effect of fishing on stocks of Pacific ocean perch was examined through an approach similar to the yield per recruit analysis that is commonly used in stock assessment. However, the model and computer program developed for this study differ from conventional methods in that they allow for estimation of exploitable biomass and population fecundity as well as yield per recruit. Data required included age-specific schedules of instantaneous natural mortality, vulnerability to fishing, mean weight, and fecundity. Annual yield to the fishery, annual production of larvae, and average exploitable biomass on hand during the year were then calculated for a population based on a constant number of female recruits, assuming different combinations of instantaneous fishing mortality (F) and age of recruitment to the fishery (t_p).

The results showed that different levels of t_p, or between-stock differences in the input parameters had very little effect on the relative trends in yield, population fecundity, and exploitable biomass with increasing F. In all cases examined, there was a sharp rise in yield as F increased from 0.0 to 0.2 and a more gradual increase for F-values greater than 0.2. Relative levels of exploitable biomass and population fecundity showed a reciprocal trend, decreasing sharply as F increased from 0.0 to 0.2, and declining more gradually for F greater than 0.2.

The value of M used in the calculations had a pronounced effect on the results. If $M = 0.1$, the costs of letting F reach 0.2 are quite high, since exploitable biomass and population fecundity would be reduced to about 40% of their virgin stock levels. If $M = 0.2$, however, the costs of letting F reach 0.2 are somewhat lower, with exploitable biomass and population fecundity declining to about 50% of their level in the virgin stock.

This preliminary analysis provided some estimates of the reductions in population fecundity that could be expected under different levels of fishing intensity, but gave no insight into the effects of this reduced fecundity on future recruitment. As a result, the analysis was carried one step further and it was assumed that, at reduced levels of population density, all compensatory changes in recruitment are mediated through increases in growth. Attendant changes in fecundity at age and age at sexual maturation would then tend to increase the level of population fecundity and recruitment, since both fecundity and maturation are related to size.

Three hypothetical levels of compensatory growth and sexual maturation were considered, and none of these were effective in restoring preexploitation levels of population fecundity when $F = 0.2$. This was true even when mean length at each age increased 5% and sexual maturation occurred a year earlier than normal. Even when F is restricted to 0.1, Pacific ocean perch would have to undergo significant compensatory changes in growth to restore population fecundity to virgin stock levels, when the stock was presumably near the replacement point (P_r) on the spawner-recruit curve.

Since Pacific ocean perch stocks are poorly adapted to extensive displacements from P_r, it was suggested that drastic action will probably be required to return them to their former levels of population fecundity, beginning perhaps with a

ban on fishing. Once the stocks approach their former levels of abundance, the harvest from both the QCS and WVI stocks should be regulated so that the catch does not exceed $0.1\hat{\beta}$, where $\hat{\beta}$ is the estimated stock biomass.

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ANALYSIS OF AGE DETERMINATION METHODS FOR YELLOWTAIL ROCKFISH, CANARY ROCKFISH, AND BLACK ROCKFISH OFF OREGON[1]

LAWRENCE D. SIX[2] AND HOWARD F. HORTON[3]

ABSTRACT

Age determination methods and their application are presented for yellowtail rockfish, *Sebastes flavidus;* canary rockfish, *S. pinniger;* and black rockfish, *S. melanops,* collected off Oregon during 1972-75. Of 25 anatomical structures examined, those compared for consistency of readings were the anal fin pterygiophore, opercle, otolith, scale, and vertebra. Various heating, staining, and microscopy techniques were applied to otoliths and scales with little success. The effect of deviation between otolith readings on survival estimates and age-length relationships is discussed. Consistency of otolith readings was generally superior to other structures for these three species. For yellowtail, canary, and black rockfishes, respectively, 71, 76, and 76% of two independent otolith readings deviated by no more than ±1 assumed annulus. Consistency of otolith readings for all three species decreased with age. Even though age estimates were not completely consistent, Chapman-Robson and catch curve estimates of survival, as well as age-length relationships, each derived from two readings of the same set of otoliths, were not significantly different at the 95% level for the three species. Age-length relationships are given for both male and female yellowtail, canary, and black rockfishes.

In 1973, yellowtail rockfish, *Sebastes flavidus* (Ayres); canary rockfish, *S. pinniger* (Gill); and black rockfish, *S. melanops* Girard, composed 41, 38, and 4%, respectively, of the total Oregon commercial trawl catch of rockfishes consisting of 19 species (Oregon Department of Fish and Wildlife[4] unpubl. data). Because little is known of the biology of these fishes, information on age, length, and weight are needed for estimates of mortality, growth, and ultimately sustainable yield.

The investigation was based on analysis of samples taken off Oregon from 1972 to 1975. The overall objective was to determine if an acceptable technique(s) could be developed for age determination of these species. Specific objectives were: 1) to determine if counts of annuli on aging structures can be reproduced consistently; and 2) to determine if deviations between successive counts of annuli significantly affect estimates of survival and the age-length relationships.

Considerable effort has been expended on age determination of commercially important species of *Sebastes* in the North Atlantic. Perlmutter and Clarke (1949) used scales to age juvenile redfish, *S. marinus,* but did not include older fish in the study because of difficulty in discerning annuli. Kelly and Wolf (1959) reported 100% agreement between independent readings of redfish otoliths with less than 10 annuli, but agreement between readings for fish from 7 to 20 + yr was only 31%. Sandeman (1961) used scales for juvenile redfish (<5 yr), but found otoliths to be superior for older fish.

In the North Pacific Ocean, the majority of research relative to our study has been conducted on the Pacific ocean perch, *S. alutus.* Alverson and Westrheim (1961) reported readability of scales for Pacific ocean perch was only fair, while Chikuni and Wakabayashi (1970) were satisfied with scales for the same species. Westrheim (1973) subsequently found that agreement between readings of Pacific ocean perch otoliths decreased from 100% for 0-zone otoliths to 26% for 19-zone otoliths. Phillips (1964) found both scales and otoliths could be used for valid age estimations for 10 species of California rockfish, includ-

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ing *S. flavidus* and *S. pinniger,* but used scales because they were obtained with less effort. Miller and Geibel (1973) preferred scales to otoliths for blue rockfish, *S. mystinus,* off California because scales allowed greater ease in back-calculation of growth. Wales (1952), working on the same species, reported that scales were easier to read than otoliths. Chen (1971) found scales were frequently regenerated on rockfish of the subgenus *Sebastomus,* so he used otoliths for age determination.

Otoliths were used to age copper rockfish, *S. caurinus,* in Puget Sound (Patten 1973) and northern rockfish, *S. polyspinis,* in the Gulf of Alaska (Westrheim and Tsuyuki 1971). There are no published reports on the life of *S. melanops,* although Miller (1961) indicated that the ages of several specimens were estimated. Westrheim and Harling (1975) used otoliths to determine age-length relationships for 26 scorpaenids in the northeast Pacific.

TABLE 1.—Structures examined from yellowtail rockfish, canary rockfish, and black rockfish with a description of their suitability for age determination.

Structure	Description
Anal fin pterygiophore	enumerable zones present
Anal spine	zones present, but not enumerable
Articular	insufficient calcification
Asteriscus	insufficient calcification
Basipterygium	zones present, but not enumerable
Ceratohyal	insufficient calcification
Cleithrum	zones present, but not enumerable
Dentary	zones present, but not enumerable
Epihyal	insufficient calcification
Hypurals	insufficient calcification
Interopercle	zones present, but not enumerable
Lachrymal	insufficient calcification
Lapillus	insufficient calcification
Maxilla	zones present, but not enumerable
Mesopterygoid	insufficient calcification
Neurocranial bones	insufficient calcification
Opercle	enumerable zones present
Pelvic fin rays	zones present, but not enumerable
Postcleithrum	insufficient calcification
Premaxilla	zones present, but not enumerable
Sagitta	enumerable zones present
Scale	enumerable zones present
Subopercle	insufficient calcification
Supracleithrum	zones present, but not enumerable
Vertebral centrum	enumerable zones present

METHODS AND MATERIALS

Most fish used in this study were sampled randomly from the commercial trawl landings in Astoria and Coos Bay, Oreg., from 1972 to 1975. Sex, length to the nearest centimeter, and weight to the nearest gram were recorded, and one or both saccular otoliths (sagittae) were extracted. Twenty-five anatomical structures (Table 1), including the anal fin pterygiophores (largest), opercles, otoliths, scales, and several anterior vertebrae were sampled from carcasses obtained from fish processing plants in Newport, Oreg., from 1974 to 1975. Juvenile fish were collected on research cruises on the Oregon continental shelf from 1972 to 1974, and by scuba and hook-and-line in Yaquina and Tillamook bays from 1973 to 1975.

Otoliths were stored in a 50:50 solution of glycerine and water and read using reflected light on a dark background utilizing a binocular dissecting microscope at 10×. Otolith sections 0.3 mm thick were obtained with a thin sectioning machine after being embedded in polyester casting resin. Scales were cleaned, dried, and mounted between glass slides or impressed on acetate cards and read using a scale projector with a 48-mm objective. Other structures, including opercles, pterygiophores, and vertebrae were heated in a detergent-water solution at 50°C for 20 min to remove adhering tissue and air dried. Opercles were examined with the naked eye and pterygiophores and vertebrae were examined by use of a binocular dissecting microscope at 10×.

One year of the life of the fish was assumed to be represented by an opaque zone followed by a hyaline zone on otoliths (Kelly and Wolf 1959; Westrheim 1973) as well as on opercles, pterygiophores, and vertebrae. A scale annulus was defined as a zone of closely spaced circuli (check) following a zone of widely spaced circuli (Van Oosten 1929; Tesch 1968). True annuli are represented by pronounced hyaline zones on otoliths and bony structures and by pronounced checks on scales. Indistinct zones or zones that are split or discontinuous were considered accessory (false) annuli. A zone that obviously interrupts the periodicity of the pattern of zonation was considered to be accessory unless it occurred in many fish in the same sample.

Consistency of readings of aging structures was measured by the ability of the reader to reproduce successive, independent counts of annuli. To insure independence there was a period of several months between most otolith readings. When the period was less than 2 wk, a five digit code number was assigned to each structure to prevent possible memorization of previous age estimations. Independent readings of yellowtail rockfish otoliths were made by two people, while those of canary and black rockfishes were made by the same person.

Age composition data were described graphically by FISHPLOT, a computer plotting routine based on the method of Hubbs and Hubbs (1953). Survival estimates were obtained by the Chapman-Robson (Robson and Chapman 1961) and the catch curve (Ricker 1975) methods. The age-length relationship of yellowtail rockfish was described by the equation $L = cA^b$, where L = length (centimeters), A = estimated age (years), and c and b are constants. The age-length relationships for canary and black rockfish were described by the von Bertalanffy growth-in-length equation with the computer program BGC-2 (Abramson 1965) using the method of least squares weighted according to sample size (Tomlinson and Abramson 1961).

A total of 71 young unsexed black rockfish, mostly young-of-the-year, were used in the age-length analysis. Their corresponding lengths were applied to both males and females, with the assumption that there were little or no sexual differences in length at these younger ages. The assumption was based on the fact that growth curves for male and female Pacific ocean perch, obtained by Westrheim (1973) for fish from Oregon to British Columbia and by Gunderson (1974) for Washington samples, were nearly identical at ages less than 6 yr.

RESULTS AND DISCUSSION

Suitability of Structures for Age Determination

Only 5 of 25 anatomical structures sampled were suitable for estimation of age. These were the anal fin pterygiophore, opercle, otolith, scale, and vertebra. The criterion used to determine suitability for aging was the presence of enumerable growth zones. Based on examination of a limited sample, most structures did not satisfy this criterion because: 1) they were not sufficiently calcified to reveal distinct growth zones, or 2) calcification was evident but growth zones were not discernible (Table 1). The above five structures were examined further to determine whether successive, independent estimates of age were consistent.

Consistency of Readings

Percent agreement between two independent counts (readings) of assumed annuli by the same person on anal fin pterygiophores, opercles, otoliths, scales, and vertebral centra sampled from the same yellowtail, canary, or black rockfish is presented in Table 2. Exact agreement ±1 assumed annulus is also given. Agreement was low for all structures and species except otoliths of canary rockfish. Agreement between otolith readings for yellowtail and canary rockfishes was superior to agreement between readings of other structures, with 71 and 97% agreement ±1 assumed annulus, respectively. For the sample of black rockfish, otoliths and opercles were equally readable with 74 and 75% agreement ±1 assumed annulus, respectively.

Means of the two readings of the five structures agreed fairly well for black rockfish, indicating that counts of assumed annuli on the structures were similar. Means were not similar for these structures from yellowtail and canary rockfishes.

A number of samples of each structure were not read due to crystallization and breakage of otoliths, regeneration of scales, and poor calcification of opercles and pterygiophores. Throughout the entire study at least one of the two otoliths was partially or completely crystallized in 23 of 1,116 (2.1%) yellowtail rockfish, 27 of 666 (4.1%) canary rockfish, and 29 of 302 (9.6%) black rockfish. There were more readable vertebral centra and otoliths than any of the other structures. Many

TABLE 2.—Estimations of age, number of readable structures, and percent agreement of two independent readings of five structures sampled from 35 yellowtail rockfish, canary rockfish, and black rockfish landed off Newport, Oreg., 1974-75.

Structure	Estimated age (yr)		No. readable	Agreement (%)	
	Min-max	Mean		Exact	±1 yr
Yellowtail rockfish					
Anal pterygiophore	9-18	12.5	29	24	59
Opercle	—	—	3	—	—
Otolith	10-18	15.2	34	24	71
Scale	8-15	11.2	32	16	59
Vertebral centrum	8-18	12.9	35	11	49
Canary rockfish					
Anal pterygiophore	7-20	9.5	33	33	76
Opercle	4-18	7.8	31	10	48
Otolith	5-22	8.9	35	77	97
Scale	7-23	10.7	32	31	69
Vertebral centrum	5-18	8.9	35	31	60
Black rockfish					
Anal pterygiophore	5-18	9.6	32	19	66
Opercle	5-18	9.2	28	39	75
Otolith	6-15	10.7	35	40	74
Scale	7-16	10.7	31	23	61
Vertebral centrum	6-18	10.3	35	14	54

opercles were not readable, especially those sampled from yellowtail rockfish, where 32 of 35 could not be used for age determination.

Consistency of otolith and scale readings subsequently was compared in a larger sample. A chi-square test for paired data corrected for continuity revealed that exact agreement between otolith readings was significantly greater than exact agreement between scale readings for yellowtail ($P<0.05$)[5] and black ($P<0.005$) rockfishes (Table 3). No significant difference occurred between readings of otoliths and scales for canary rockfish ($P>0.90$). Percent agreement between first readings of both structures for all three species was low.

TABLE 3.—Percent agreement in estimates of age between first and second readings of the same structure and between first readings of different structures (otoliths and scales) sampled from the same yellowtail rockfish, canary rockfish, or black rockfish caught off Oregon, 1974-75.

	Within structures						
	Otolith		Scale		Between structures		
Species	Exact	±1	Exact	±1	Exact	±1	*N*
Yellowtail rockfish	42	80	26	60	14	53	89
Canary rockfish	37	73	36	70	15	39	91
Black rockfish	48	81	26	54	11	43	98

In terms of consistency of readings, the otolith is the best structure of those examined for age determination of yellowtail, canary, and black rockfishes; yet, even this method is questionable. Deviations of readings of yellowtail rockfish otoliths by two readers generally increased with age of the fish (Figure 1). For canary rockfish otoliths read twice by the same person, deviations of readings initially increased and then stabilized with increasing age (Figure 2). Deviations of readings of black rockfish otoliths read twice by the same person also increased with age of the fish (Figure 3). The distribution of deviations is skewed considerably in the positive direction, indicating that the second reading was substantially lower than the first. For our largest sample of 322 yellowtail rockfish, 481 canary rockfish, and 357 black rockfish, respectively, 71, 76, and 76% of the two readings deviated by no more than ±1 assumed annulus. In a study on Pacific ocean perch by Westrheim (1973), 85% of two otolith readings by different people deviated by no more

[5]Probability of a greater chi-square value.

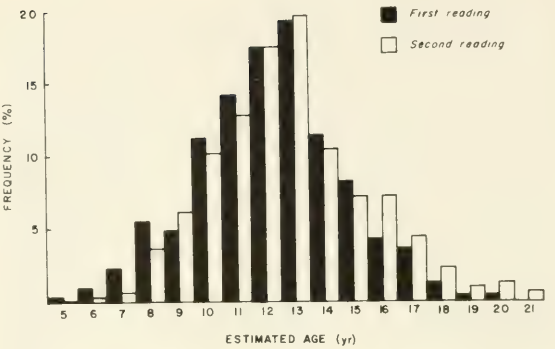

FIGURE 1.—Age composition of 322 yellowtail rockfish obtained by two independent readings of their otoliths; specimens were collected from fish processing plants in Astoria and Coos Bay, Oreg., 1973-74.

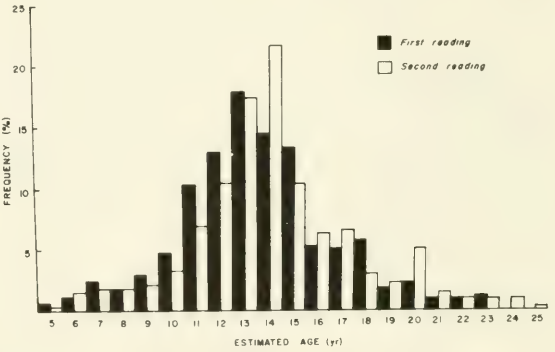

FIGURE 2.—Age composition of 353 canary rockfish obtained by two independent readings of their otoliths; specimens were collected from fish processing plants in Astoria and Coos Bay, Oreg., 1974.

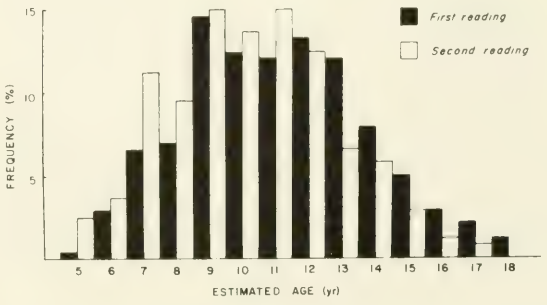

FIGURE 3.—Age composition of 242 black rockfish obtained by two independent readings of their otoliths; specimens were collected from fish processing plants in Astoria and Coos Bay, Oreg., 1974.

than ±1 zone. Kelly and Wolf (1959) reported 59.7% agreement ±1 yr for otoliths of 7–20+ yr-old redfish.

Several explanations exist for the observed deviations between readings. Due to the presence of split zones and the irregularity of the marginal areas on older rockfish otoliths, different readings may be obtained from different areas of the same otolith. There are eight major marginal areas on otoliths that can be used in age determination (Figure 4); two or three generally give superior results depending on the species in question. However, these favored areas are not consistently readable from one otolith to the next in any sample. Therefore, there is no specific area that can be used consistently on all the otoliths, making it possible that two different areas could be read on two independent readings of the same otolith. Indeed a comparison of areas used by readers A and B for yellowtail rockfish otoliths showed that of the readings that disagreed, 71% were made on different areas of the otolith, whereas, of the readings that agreed, only 56% were made on different areas.

Discrepancies in counts of annuli also are probably a function of the difficulty in defining the type of outer edge on otoliths. If an otolith had two opaque zones, each followed by a hyaline zone, plus an additional opaque zone on the outer edge, then an age of 2 was assigned. If an additional hyaline zone existed on the edge of the above otolith, then an age of 3 was assigned. But since the zones on the outer edge of older rockfish are indistinct because of slow growth at older ages, it is conceivable that discrepancies of 1 yr could exist between independent readings of the same area of a particular otolith.

A third cause of discrepant counts is that entire samples of otoliths were often exceptionally opaque, or, conversely, transparent, possibly due to the storage medium and/or length of storage. Annuli on otoliths such as these are difficult to distinguish.

Because one could question the use of only two readings to assess the consistency of otolith readings, a sample of 198 yellowtail rockfish otoliths was read independently three times with a week between readings. A chi-square test for independent data corrected for continuity indicated no significant differences among the three agreement statistics ($P>0.75$). In this case, consistency of readings was not changed by the addition of a third reading.

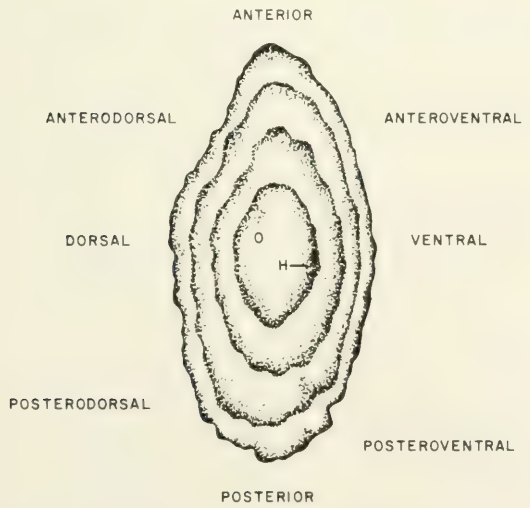

FIGURE 4.—Drawing of the right otolith (sagitta) from a 4-yr-old black rockfish as seen under reflected light on a dark background showing the marginal areas used in age determination (O-opaque zone; H-hyaline zone).

Validity of the Otolith Method

Until the data needed for validation can be collected, it is assumed for the purposes of this study that one opaque and one hyaline zone are laid down each year on otoliths of rockfishes in Oregon. Van Oosten (1929) and Graham (1956) listed methods used to provide indirect evidence of the validity of age readings of scales and other structures. The commonly applied methods are observation of a dominant year class over a period of years, and analysis of seasonal changes of the margin of some anatomical structure. Westrheim (1973) was able to follow the yearly progression of a dominant year class of *Sebastes alutus* for a period of several years and also demonstrated, by examination of the marginal zones on the otolith, that the hyaline zone is formed annually on juvenile fish. Kelly and Wolf (1959) found that one opaque and one hyaline zone are laid down each year on otoliths of young *S. marinus*.

Unfortunately, similar tests could not be conducted in this study owing to the absence of any obviously dominant year classes in the fish sampled and to the inadequate samples of young fish from a sufficient number of months throughout the year to permit demonstration of the seasonal changes in the margin of the otolith. Otoliths from older rockfish are not suitable for

this method, because zones on the outer edge are narrow and therefore difficult to distinguish until late in the growing season. Moreover, because of the irregular growth of otoliths of older rockfish, different marginal areas provide different results.

Otolith Sections

Results indicate that consistency of otolith readings is superior to that of scales or other structures for the three species of rockfishes studied, but agreement of otolith readings still may be unsatisfactory. Otoliths were sectioned to try to improve consistency of readings. Blacker (1974) noted that annuli are laid down only on the proximal (internal) surface of the otolith during later years in the life of fishes such as sole, *Solea solea;* plaice, *Pleuronectes platessa;* turbot, *Scophthalmus maximus;* redfish, *Sebastes* sp.; and horse mackerel, *Trachurus trachurus*. These annuli are not seen when the distal surface of the otolith is used for age determination and the investigator underestimates the age of the fish.

Exact agreement between readings of whole and sectioned otoliths of canary rockfish (37 vs. 21%) differed by 16 percentage points (Table 4). A chi-square test for paired data corrected for continuity revealed that there was a significant difference between the two ($P<0.025$). Percent agreement between first readings of whole and sectioned otoliths was low with a value of 51% ± 1 assumed annulus. The similarity of the mean estimated ages indicates that the phenomenon reported by Blacker (1974) probably does not occur in canary rockfish otoliths. Ages were not substantially underestimated by reading the distal surface of the whole otolith.

Sectioning did not improve consistency of readings of canary rockfish otoliths. Moreover, it is not possible to follow specific annuli completely around the sectioned otolith to determine if an assumed annulus is split. Whole otoliths allow the reader a choice of marginal areas to read, whereas sections do not.

Additional treatments were applied to otoliths and scales with little success (Table 5).

TABLE 4.—Percent agreement between first and second readings of whole otoliths and between first and second readings of sectioned otoliths, and percent agreement between first readings of whole and sectioned otoliths of canary rockfish caught off Oregon, 1974.

	Within technique		Between techniques
Agreement	Whole	Sectioned	(Whole vs. sectioned)
Exact	37	21	21
± 1	71	57	51
N	91	91	91
Mean estimated age	14.0	14.7	

TABLE 5.—Treatments applied to otoliths and scales of yellowtail, canary, and black rockfishes captured off Oregon during 1972-75.

Treatment	Description	Result
	Otoliths	
Baking	Lawler and McRae (1961)	Resolution not improved
Burning	Christensen (1964)	Difficult to obtain consistent effect
Scanning electron microscopy	Liew (1974), Blacker (1975)	Impracticable to view entire otolith in detail
Surface microscopy	Smith (1968)	Zones indistinct
Alizarin red S staining	In 1% KOH to obtain purple color	Stain not readily absorbed
Methyl violet stain	Albrechtsen (1968)	Stain absorbed, but zones indistinct
Silver nitrate stain	1% aqueous solution	Stain not absorbed
	Scales	
Polarized light microscopy	Kosswig (1971)	Zones near focus indistinct

Effect of Deviations of Otolith Readings on Biological Information

Age Composition

The frequencies of two independent readings of yellowtail rockfish otoliths made by different readers generally correspond for ages 9-15 (Figure 1). Correspondence is lower for younger and older age-groups. The two distributions are approximately normal with means of 12.2 and 12.8 yr, respectively. Figure 5 graphically demonstrates that the means are not significantly different because the 95% confidence intervals for the means overlap. For the two distributions, the standard deviations are similar and the ranges are equal, but the minimum and maximum values disagree by 1 yr (Figure 3).

Frequencies of age readings for canary rockfish derived from two independent readings by the same person correspond over most of the ranges of ages (Figure 2). Greatest discrepancies occurred at ages 11, 14, and 20. Again the distributions are approximately normal with means of 13.6 and 14.2 yr for first and second readings, respectively. The means are not significantly different at the 95% level (Figure 5). The standard deviations are similar, while the maximum ages disagree by 2 yr.

Otolith reading frequencies for two independent readings by the same person for black rockfish correspond closely for ages 9-12. There is less agreement for other ages (Figure 3). The

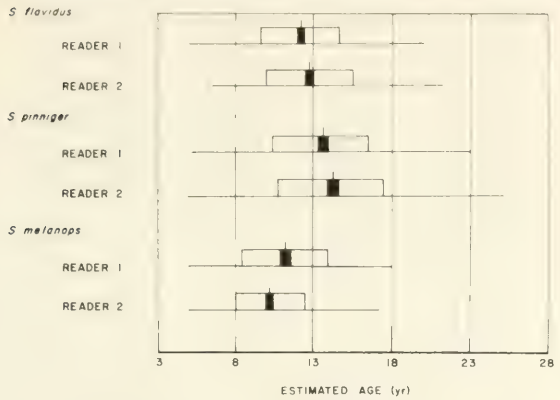

FIGURE 5.—Mean (vertical line), range (horizontal line), standard deviation of the mean (white bar), and 95% confidence intervals about the mean (black bar) for two otolith age readings of yellowtail rockfish, canary rockfish, and black rockfish landed in Oregon, 1973-74.

distributions are approximately normal with means of 11.1 and 10.2 yr, respectively, for first and second readings. Figure 3 shows the means to be significantly different at the 95% level. The standard deviations of the two distributions differ more for this species than for yellowtail and canary rockfishes. Ranges of the two distributions are similar (Figure 5).

Survival

Estimates of survival obtained by two methods generally correspond for all species and readings, although Chapman-Robson estimates were consistently lower than catch curve estimates (Table 6). At the 95% level none of the paired estimates from the two readings were significantly different, as shown by the overlap of confidence intervals. Differences between survival estimates calculated from readings of the same otoliths were greatest for yellowtail rockfish and smallest for canary rockfish by either the catch curve or the Chapman-Robson method; yet, on the average, differences between catch curve estimates for the two readings were greater than those obtained by the Chapman-Robson method (Table 6). The differences between catch curve estimates were 0.11, 0.015, and 0.093 for yellowtail, canary, and black rockfishes, respectively, while differences between Chapman-Robson estimates were 0.051, 0.031, and 0.051, respectively.

Age-Length Relationship

The age-length relationships derived from two otolith readings for yellowtail rockfish were described by the equation $L = cA^b$ (Figure 6). Fitted lengths-at-age for the first reading were slightly higher than those for the second reading, but 95% confidence limits of the estimates of constants c and b overlap considerably for the first and second readings (Table 7). Little or no overlap of confidence limits for constants c and b exists for males and females for either the first or second readings (Table 7), indicating a significant difference between the age-length relationships by sex for yellowtail rockfish. Age-length data for yellowtail rockfish were initially applied to the von Bertalanffy growth-in-length equation, but were not well described by this equation due to the lack of young fish in the samples.[6]

Age-length relationships for male canary rockfish based on two independent readings are nearly identical (Figure 7). Growth curves for females are similar (Figure 7), but discrepancies exist at older ages where fitted lengths for the first reading were higher than those for the second.

[6]The von Bertalanffy equations derived from two readings of yellowtail rockfish otoliths were:

Males—Reading 1: $l_t = 47.96[1 - \exp(-0.16(t + 4.01))]$
Reading 2: $l_t = 46.34[1 - \exp(-0.27(t - 1.03))]$

Females—Reading 1: $l_t = 55.47\ [1 - \exp(-0.14(t + 3.19))]$
Reading 2: $l_t = 53.81\ [1 - \exp(-0.19(t - 0.24))]$.

TABLE 6.—Survival estimates based on two independent readings of the otoliths of yellowtail rockfish, canary rockfish, and black rockfish landed in Oregon, 1973-74.

	Chapman-Robson			Catch curve				
Species	Estimate	SE	95% conf. limits	Estimate	SE	95% conf. limits	R^2	Ages used
Yellowtail rockfish:								
Reading 1	0.54	0.04	0.46-0.61	0.60	0.04	0.49-0.70	0.95	14-18
Reading 2	0.59	0.03	0.52-0.65	0.71	0.05	0.59-0.82	0.90	14-18
Canary rockfish:								
Reading 1	0.67	0.03	0.62-0.72	0.73	0.04	0.65-0.80	0.86	15-23
Reading 2	0.70	0.02	0.65-0.75	0.74	0.04	0.66-0.82	0.85	15-23
Black rockfish:								
Reading 1	0.60	0.03	0.54-0.66	0.67	0.02	0.62-0.72	0.98	12-17
Reading 2	0.55	0.04	0.47-0.63	0.58	0.03	0.52-0.64	0.97	12-17

TABLE 7.—Estimates of parameters describing the age-length relationship for yellowtail rockfish, canary rockfish, and black rockfish based on two independent readings of their otoliths. The 95% confidence limits for the estimates are in parentheses.

Parameters	First reading	Second reading
♂ yellowtail rockfish:		
c	28.00	28.41
	(25.96-30.03)	(26.37-30.45)
b	0.18	0.17
	(0.15-0.21)	(0.14-0.20)
♀ yellowtail rockfish:		
c	25.08	23.66
	(23.05-27.12)	(21.62-25.71)
b	0.26	0.29
	(0.23-0.30)	(0.25-0.32)
♂ canary rockfish:		
L_∞	53.60	53.30
	(52.38-54.82)	(52.14-54.46)
k	0.19	0.18
	(0.17-0.21)	(0.16-0.20)
t_0	0.68	0.54
	(0.39-0.97)	(0.25-0.83)
♀ canary rockfish:		
L_∞	60.95	57.43
	(58.09-63.81)	(55.90-58.96)
k	0.15	0.18
	(0.12-0.17)	(0.15-0.20)
t_0	0.54	0.90
	(−0.03-1.11)	(0.49-1.30)
♂ black rockfish:		
L_∞	50.30	52.03
	(49.07-51.53)	(50.48-53.58)
k	0.23	0.22
	(0.21-0.26)	(0.19-0.25)
t_0	−0.46	−0.44
	(−0.65)-(−0.28)	(−0.62)-(−0.26)
♀ black rockfish:		
L_∞	57.83	58.78
	(55.30-60.36)	(56.43-61.13)
k	0.17	0.18
	(0.14-0.19)	(0.15-0.20)
t_0	−0.74	−0.56
	(−0.99)-(−0.49)	(−0.77)-(−0.35)

This difference exists because the first reading was generally lower than the second, and readability decreased with age. Interval estimates of the von Bertalanffy constants L_∞, k, and t_0 for first and second readings for males are comparable (Table 7). Greater differences occur between estimates of the parameters for first and second readings for females, although interval estimates still overlap. For males and females for the first reading, there is no overlap of interval estimates for L_∞, slight overlap for k, and considerable overlap for t_0 (Table 7). Similarly, for males and females for the second reading, there is no overlap of interval estimates for L_∞, and considerable overlap of interval estimates for k and t_0. This indicates that differences in growth exist.

Growth curves for male black rockfish derived from two otolith readings are similar (Figure 8), although discrepancies existed between fitted lengths at older ages. The same is true for the age-length relationship for females (Figure 8). Interval estimates of all three von Bertalanffy constants overlap considerably (Table 7), indicating no significant differences between growth curves obtained from the two readings. For males and females for the first reading, there is no overlap of interval estimates for L_∞ and k, and considerable overlap for t_0. For males and females for the second reading, there is no overlap of interval

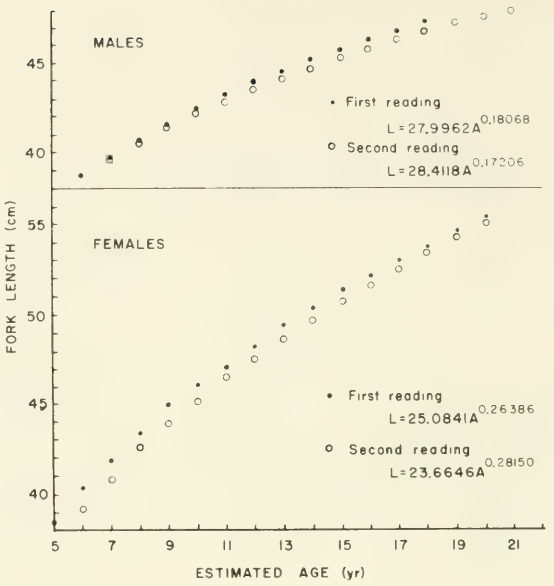

FIGURE 6.—Age-length relationships for yellowtail rockfish derived from two independent readings of their otoliths collected from Oregon samples, 1973-74.

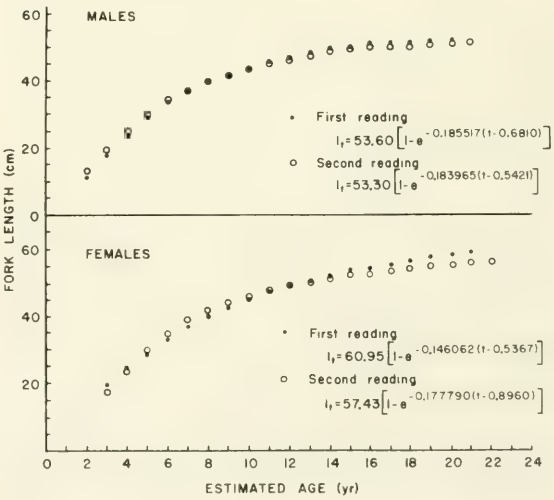

FIGURE 7.—Age-length relationships for canary rockfish derived from two independent readings of their otoliths collected from Oregon samples, 1972 and 1974.

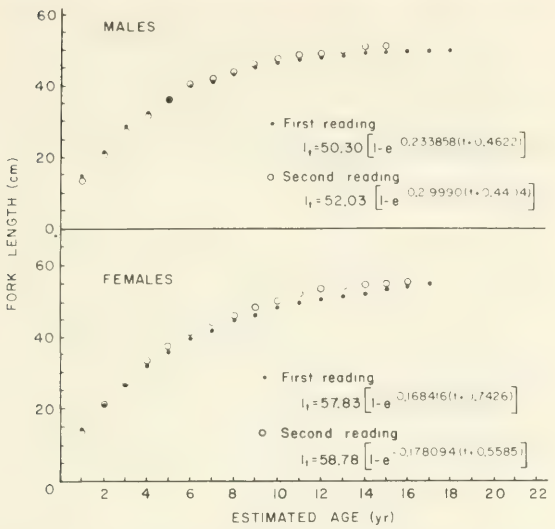

FIGURE 8.—Age-length relationships for black rockfish derived from two independent readings of their otoliths collected from Oregon samples, 1973-75.

estimates for L_∞, slight overlap for k, and considerable overlap for t_0. As was found for yellowtail and canary rockfishes, sexual differences in growth of black rockfish are apparent.

Further support of the otolith method may be evidenced by a comparison of mean lengths-at-age obtained in this study with those of other investigators. Phillips (1964) and Westrheim and Harling (1975) reported mean lengths similar to those obtained in this study for yellowtail rockfish (Table 8). A similar correspondence of canary rockfish lengths does not exist, where an increase of values from north to south is noted. This analysis is limited by small sample sizes and could further be complicated by geographical differences in growth reported to exist for other species of rockfishes in the Northeast Pacific (Westrheim and Harling 1975).

In summary, the observed deviations between otolith readings produced slightly different estimates of survival and of age-length relationships, although these differences were not statistically significant. The otolith method is the most reliable of those analyzed and we believe, with some reservations, that it can be used reliably for management purposes. The reader should be cautioned that contrary to the results of the statistical test, some of the survival estimates appear to be substantially different (Table 6). Possibly a Type II error exists (Snedecor and Cochran 1967), i.e., the statistical test shows no significant difference when, in fact, one exists. We believe that, for the most part, the observed deviations between readings are minor; moreover, with the collaboration of two or more trained readers, consistency of age determinations can be improved.

Further studies establishing the validity of the technique are warranted. This may be made possible by analysis of the marginal growth of the otoliths of juvenile rockfish. By providing evidence that an opaque and an adjacent hyaline zone truly constitute an annulus, accuracy of otolith age determinations will be ensured.

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TABLE 8.—Mean length (centimeters) at selected ages of yellowtail rockfish and canary rockfish from British Columbia, Oregon, and California. Numbers of fish are shown in parentheses.

		British Columbia (Westrheim and Harling 1975)		Oregon (This study—reading 1)		California (Phillips 1964)
Species	Age	Male	Female	Male	Female	Sexes combined
Yellowtail rockfish	5	27.1 (16)	27.6 (10)	—	30.0 (1)	31.9 (116)
	10	42.3 (4)	41.0 (2)	42.9 (15)	46.6 (19)	43.0 (48)
	15	46.6 (18)	49.2 (7)	46.1 (17)	50.4 (8)	50.4 (6)
	20	47.6 (8)	—	—	53.0 (1)	—
Canary rockfish	5	22.5 (1)	23.5 (1)	29.0 (8)	29.2 (26)	31.9 (128)
	10	—	38.5 (1)	44.7 (11)	48.0 (6)	46.8 (57)
	15	—	—	49.2 (32)	52.4 (12)	56.5 (7)
	20	50.5 (1)	—	51.0 (2)	56.0 (6)	—

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PREDATOR-PREY INTERACTIONS IN SCHOOLING FISHES DURING PERIODS OF TWILIGHT: A STUDY OF THE SILVERSIDE *PRANESUS INSULARUM* IN HAWAII[1]

PETER F. MAJOR[2]

ABSTRACT

Observations of free living and captive silversides were made in Kaneohe Bay, Hawaii, in October and November 1972 and September 1973. The silversides demonstrated changes in schooling behavior associated with changes in light levels during the periods of twilight. During morning twilight, individual silversides formed schools, which in some areas moved from deep water to shallow water over reefs. All silversides remained in large inactive schools in shallow water or along the edge of channels throughout the day. During evening twilight, schools left the reef and/or broke up, with individual silversides spreading out to feed near the surface. Predation upon the silversides, as evidenced by their jumping behavior, was most intense during the twilight periods as schools formed and broke up. Captive silversides, when not in the presence of predators, tended to increase their interfish distance when in diurnal schools. The formation and breakup of schools of these silversides appear to be very similar to behavioral patterns of related and unrelated species of fish in many parts of the world. The formation and break up of silverside schools appear to be related to the threat of predation, the availability of the silverside's food, and the visual sensitivity and thresholds of both the silversides and their predators.

Daily twilight or crepuscular periods are critical ones with respect to predator-prey interactions between many species of fishes, at least in tropical regions of the world. Hobson (1968, 1972), Collette and Talbot (1972), and Domm and Domm (1973) demonstrated the importance of twilight periods on behavioral changes in reef fishes. Hobson (1968, 1972, 1974) suggested that such transitions in behavior are shaped by the threat of predation.

Predation pressure is also clearly a factor in the evolution of schooling behavior in prey species (Breder 1959, 1967; Hobson 1968; Shaw 1970; Radakov 1973). Most reef fishes hide from their predators amongst the interstices of the coral reef. Many surface and open water prey species lack such hiding places and appear to form schools as a means of cover seeking (Williams 1964, 1966), the school serving as a mobile biological refugium especially during daylight hours. During evening twilight periods many such schools break up with individuals spreading out to feed. During morning twilight periods individuals once again form schools (Hobson 1968, 1972, 1973; Hobson and Chess 1973).

Vision has been shown to be important in the maintenance of schools (Woodhead 1966; Hunter 1968; Shaw 1970; Radakov 1973). In addition, Munz and McFarland (1973) indicated that the behavioral changes of tropical marine fishes during periods of twilight are due to shifts in the visual sensitivity of these fishes with changes in light levels.

The objectives of this study were to determine if schools of the Hawaiian silverside, the iao, *Pranesus insularum*, broke up and reformed in response to light levels occuring during twilight, and to determine how the activity of predators of this species of silverside was related to this behavior.

Study Sites

Field observations were made at two locations within Kaneohe Bay, along the island of Oahu in the Hawaiian chain. These sites were a 10,000 m^2 area of flat reef (water depth $\leq$2 m at high tide) immediately adjacent to the east side of Lilipuna Pier (Dock), and a 2,500 m^2 area near the central portion of a dredged out (to a depth of 2-3 m)

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"lagoon" adjacent to the Hawaii Institute of Marine Biology (HIMB) on Coconut Island. The northern edge of the reef adjacent to Lilipuna Pier drops abruptly into a 3- to 10-m deep channel, while the southern side is adjacent to the shore.

The reef and channel area near Lilipuna Pier are open to the effects of wind and waves within Kaneohe Bay throughout the year. Occasionally, the winds abate or shift and the bay's surface becomes calm and glassy. The observations reported here could only be made at such times when the estimated wind velocity was less than 2.6 m/s (5 knots). At night near the end of the pier a fixed low intensity incandescent light bulb casts an arc of light out over a small area in the channel. Observations were not made within the area encompassing this arc of light. The waters in the HIMB lagoon are usually calm or only slightly rippled, being protected by a vegetation covered coral rubble peninsula on its normally windward side and thicker, higher, vegetation on its island or leeward side.

Kaneohe Bay is rimmed at approximately 1.6 km inland by mountains that rise to 762-960 m. Throughout each day, dense clouds usually form along these mountains, occluding the sun during the late afternoon. This often results in twilight conditions occurring earlier than would normally be predicted for the bay's position of latitude and longitude.

METHODS

The prey species of fish observed in this study was *P. insularum,* approximately 20-60 mm SL and approximately 0.03-2.45 g wet weight. Observations of the silverside's behavior were made during calm periods in October (7 days) and November (3 days) 1972 and September (5 days) 1973. All observations were made visually from a height of 0-3 m above the surface of the water. The morning observations commenced approximately 115 min prior to the time of sunrise. The evening observation period terminated about 60 min after the time of sunset.

The only attribute monitored quantitatively during the course of the observations was the jumping escape behavior of the silversides in response to attacking predatory fishes. Enumerating the jumps became a shorthand method of quantifying the number of predatory attacks in the calm areas studied because jumping was observed to be the primary means of escaping predators once an attack occurred. *Pranesus insularum* was the only prey species observed to jump in the above areas during the periods of this study. The success of predators at capturing prey during the attacks was not determined. Hobson (1968) used a similar method to quantify the number of times leaping predatory cabrilla, *Mycteroperca rosacea*, attacked flatiron herring, *Harengula thrissina*, in the Gulf of California.

During periods of darkness or reduced light, when visual observations under existing light were not possible, jumping by schools of prey could be heard within the areas studied by careful listening; this could only be done when there was no wind and the surface of the water was calm. The time at which schools broke up or reformed during twilight was estimated by listening to changes in the sound of jumps made by multiple and single prey close by, or with a flashlight beam which was quickly turned on and off in one spot, or swept rapidly across the surface of the water from above, and/or held underwater within 0.3 m of the surface. Whether the silversides were schooling or spread out could be readily determined when the fish were illuminated by the beam of light.

Light measurements were made above the surface of the water with a photometer (Weston Ranger 9 universal exposure meter).[3] Readings taken with this photometer were compared with those made with a Gossen foot-candle meter and a Spectra-Combi 5000 Model photometer (Photo Research, Burbank, Calif.). The readings obtained during twilight periods were comparable to those given by Brown (1952).

The observations and events reported here are related to the time of sunrise, sunset, and the periods of morning and evening civil and nautical twilight. The two periods of twilight are defined by the angular distance of the sun below the horizon, 0° to −6° for civil twilight, and −6° to −12° for nautical twilight. Fish respond directly to the amount and type of light present, which is influenced by astronomical as well as local environmental conditions. However, the use of these terms and that of the corresponding angular distance of the sun below the horizon is of immense value when comparing the observations of many investigators working in different loca-

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

tions at different times of the year and under different environmental conditions.

BEHAVIOR OF FREE-LIVING SILVERSIDES

Between sunrise and sunset each day hundreds to thousands of individual silversides could be observed in large, often elongated, schools along Lilipuna Pier and other structures over shallow reefs, along the edge of reefs, and in quiet protected waters such as the HIMB Lagoon. At times the silversides remained in the shadow of structures or overhanging vegetation, rarely venturing into sunlit water. The schools were located just under the surface of the water, with individuals often forming single or multitiered layers. The schools as a whole were largely stationary and inactive except for the occasional individual that darted out from and immediately returned to a school. These individuals appeared to be feeding, snapping at objects which I could not see when they left the school. While in the large inactive schools, individuals about one-half to two body lengths apart were randomly oriented to one another. However, upon the approach of a predator or potential predator, or when attacked, the individuals rapidly became polarized, often less than a body length apart as the school maneuvered about the predator(s) in well coordinated patterns.

When a predator slowly approached a school of silversides it frequently penetrated into the school. However, as the predator moved into and through a school, the silversides split into two or more smaller groups which passed around to the sides of the predator to reunite behind and along the path just traversed by the predator. This maneuver resulted in the formation of a void or halo of clear water around the entire predator as it moved through the school. This halo was estimated to average about one to two predator body lengths in width in any direction from the predator. Similar behavior has been reported and illustrated by Breder (1959), Nursall (1973), and Radakov (1973). When a predator actually attacked, it usually dashed at high speed toward an individual in or near a school or into a segment of a school. When attacked, individuals in the immediate area of the predator jumped out of the water as they radiated out and away from the path of the predator. In a larger school, silversides at increasingly greater distances from the attacking predator jumped less, the jump(s) grading into evasive swimming; and in some instances, little or no initial response was made by individuals some distance from the predator.

As jumping silversides reentered the water they realigned with other silversides that had jumped or evaded by swimming. At the same time there was a general, though somewhat belated, movement of individuals around into the wake of the rapidly moving predator. When an attack was prolonged, as when a predator chased an individual or small group of silversides, a large school often formed a number of smaller schools, which occasionally coalesced later. Frequently, jumping and/or evading individuals or segments of the attacked school joined with one or more other schools which were usually nearby but unaffected by the predator(s).

When a predator, such as a barracuda, attacked from a horizontal direction, the silversides usually had a strong lateral component to their jumps. Such jumps usually occurred at a shallow angle just above the surface and less than 45° to the surface. When attacked from directly below, initial jumps tended to have a somewhat more vertical than horizontal component, being greater than 45° to the water's surface. Distances covered during single horizontal jumps were not measured, but may have been as great as 5-10 times an individual's body length; several meters were spanned during a series of jumps.

When more than one predator simultaneously approached or attacked a school of silversides, evasive maneuvering and jumping became confused. The more rapidly increased numbers of predators approached or attacked, the more "disorganized" the silverside's evasive response appeared to become.

In Kaneohe Bay the most common diurnal predators observed attacking and chasing silversides were barracuda, *Sphyraena barracuda*; blue jack, *Caranx melampygus*; leatherjacket, *Scomberoides lysan*; and lizardfish, *Saurida gracilis*. Needlefish, *Tylosurus* sp., were also observed near silverside schools, but attacks were not seen. During the day, and particularly during the evening twilight period, the jack, *Caranx ignobilis*, may also have been a predator. This jack readily attacked silversides in field and cement enclosures. Recently ingested silversides were occasionally found in the stomach contents of

young scalloped hammerhead shark, *Sphyrna lewini* (45-90 cm TL), caught by gill net at night in the channels of Kaneohe Bay.

Solitary barracuda and needlefish slowly cruised along just under the surface of the water when they were near schools of silversides. When stalking, they usually remained relatively motionless as they drifted or used slow caudal fin undulations to scull along the surface. The barracuda attacked by quickly dashing, usually horizontally, a short distance towards an individual or school of silversides.

Individuals or schools of jacks and leatherjackets usually swam near the bottom in the lagoon or at some midwater depth in the deeper channels near Lilipuna Pier. Individuals of these species slowly approached or rapidly attacked the silversides, usually at an angle of about 45° to the surface. They immediately retreated towards the bottom after their approach or attack.

Lizardfish are cryptically colored, solitary benthic "sit and wait" predators. When a school of silversides swam over a lizardfish, it usually dashed at an angle nearly perpendicular to the surface, or at an angle greater than about 45° to the surface as it approached the silversides.

Because the silversides were located just under the surface of the water, the attacks by their predators could usually be detected in one or both of two ways. The momentum of a rapidly moving predator often carried it clear out of the water during an attack. This was particularly evident during attacks made in a vertical direction. If the predator turned as it approached the surface, its body and/or caudal fin usually created a boil of water at the surface, which often erupted with a popping sound into a splash or spray of water. If it was calm, a boil of water often left a small area of residual foam bubbles as concentric circles moved out across the water. When chases occurred along or near the surface, the predators often left a wake of disturbed water and froth to mark its path of pursuit.

In the Lilipuna Pier area an infrequent diurnal aerial predator was also observed. One to four common noddies, *Anous stolidus pileatus*, remained near or on the pier and flew to the areas of jumping silversides and attempted to catch them while the fish were still at the surface. Noddies were more successful at catching silversides when predatory fish attacked and then chased the silversides along the surface.

BEHAVIOR OF CAPTIVE SILVERSIDES

Over 100 h of observations of captive silversides in net enclosures (3 m × 3 m × 3 m deep to 6.1 m × 6.1 m × 2 m deep) in the lagoon in Kaneohe Bay and in a circular cement tank (9 m in diameter and 3 m deep with an underwater viewing window) were made during day and night periods. Within several days after introduction into the enclosures that lacked predators, the individuals in the schools of silversides slowly increased their interfish distances from less than one or two body lengths (as seen in the field) up to distances of 5-10 body lengths or more. Although the individuals were often randomly aligned with respect to each other, they did not lose their polarity to one another when a school moved. Individuals occasionally fed during the day, much as they did when free in the field. However, they did not dash out towards an object and immediately return to a school. When one or more predators, such as jacks or barracuda, were introduced into an enclosure the schools tightened as interfish distances between silversides decreased to less than one to two body lengths. Individuals continued to dart out from the relatively stationary and motionless schools, much as they did in the field. If attacks or approaches were not initiated by a predator, the schools loosened as interfish distances increased once again. These distances were not as great as they had been prior to the introduction of the predator(s). Feeding continued until approaches or attacks occurred. When approached, schools split and formed a halo around the predator as they moved to the rear of the predator to reform a school again. When attacked, individuals jumped out of the water and across the surface, away from the predator. The behavior of individuals and schools of silversides in the enclosures was much the same as that observed in the field, as described above.

During evening twilight periods, interfish distances increased as individuals in the schools spread out across the surface. During the twilight period, I could see the prey silhouetted against the evening sky, but not the predators against the bottom. As darkness increased, it rapidly became impossible to see the silversides as well, although the boils of water and splashes made by an attacking predator and the return of jumping prey into the water could be heard. During morning

twilight, interfish distances decreased as polarized schools once again formed and moved in coordinated patterns as they did in the field.

Silverside Jumping Activity Patterns

Morning Twilight

In the Lilipuna Pier area prior to nautical twilight, I could hear jumping silversides and the "pop" associated with attacking predators striking the water's surface approximately 20 min after the observation periods had commenced and 95 min prior to sunrise (Figure 1). These jumps were made primarily by individual fish in close proximity to the pier in the channel near the edge of the reef. Jumping occurred later by increasingly larger numbers of individuals in schools at the easternmost end of the observation area. Jumps occurred initially near the edge of the reef, moved toward, then turned northwest parallel to and along the shore, finally spreading out over the reef and toward the pier. These attacks by predators and jumps of silversides sequentially traced three sides of the perimeter of a rectangle defining the east, south, and west boundaries of the observed area near the pier. Attacks and jumps in shallow water over the reef predominated after the beginning of nautical twilight, and by sunrise all attacks and jumping occurred within a few meters of the pier. Peak activity in shallow reef and deep channel water was recorded just after the beginning of civil twilight and steadily decreased to midday levels (Figure 1).

The only predators observed to attack the silversides over the reef in the early morning were lizardfish. Blue jacks and barracuda were observed in the channel and occasionally over the reef near sunrise and during the late morning.

In the lagoon area, jumps in the central deeper area of the lagoon were initially recorded 45 to 50 min before sunrise (Figure 1). As twilight progressed, jumping was eventually seen in narrow bands of shallow water along the sides of the lagoon, but occurred infrequently. Barracuda and jacks were the principal early morning predators, although lizardfish were also observed attacking the silversides. Since the shallows were relatively small in area, most of the silversides were concentrated over the central deeper water of the lagoon. A period of increased jumping activity did not occur in the lagoon during twilight as it did near the pier.

Light meter readings of 0.096-0.402 foot candle (Table 1) were made in 1973 during the time (18-24 min before sunrise, i.e., the time of civil twilight) when silversides were in the process of forming schools, especially in the lagoon area. Initial schooling became noticeable (individuals moving closer together, becoming more cohesive and polarized when swimming as they did during the day) in 1972 and 1973 as early as 44-23 min before sunrise and was completed as late as 33-18 min before sunrise (Table 2). Silversides then remained in schools throughout the day.

In summary, during the morning, predator attacks and silverside jumping could not be detected until 95 min before sunrise at the pier and 50 min before sunrise in the lagoon. Deep-water attacks were initially noted for individual silversides, but subsequently increased numbers of jumps were recorded in shallower water for increasingly larger schools, especially near the pier. During the time peak jumping occurred (30-10 min before sunrise), silversides were forming cohesive polarized schools (44-18 min before sunrise, mean 29.4 min).

TABLE 1.—Light levels (light meter readings in foot candle) and the breakup and formation of schools of silversides.

Type of activity	Author	Location	Species	Light levels		No. of readings	Remarks
				Mean	Range		
Breakup of schools	Steven 1959	West Indies	*Hepsitia stipes*	0.06	0.07-0.05	2	Fish in aquariums indoor with windows and door closed, no artificial light. Watched until nightfall.
	Shaw 1961	Marine Biological Laboratory, Mass.	*Menidia*	0.12	0.35-0.03	14	Experimental; gradual reduction of light until school began dispersing. Used neutral density filters.
	This report Sept. 1973	Kaneohe Bay, Hawaii	*Pranesus insularum*	0.21	0.402-0.035	3	Field, during evening twilight.
Formation of schools	This report Sept. 1973	Kaneohe Bay, Hawaii	*Pranesus insularum*	0.18	0.402-0.096	4	Field, during morning twilight.

[1]One-way analysis of variance (ANOVA) of all light meter readings ($P = 0.57$).

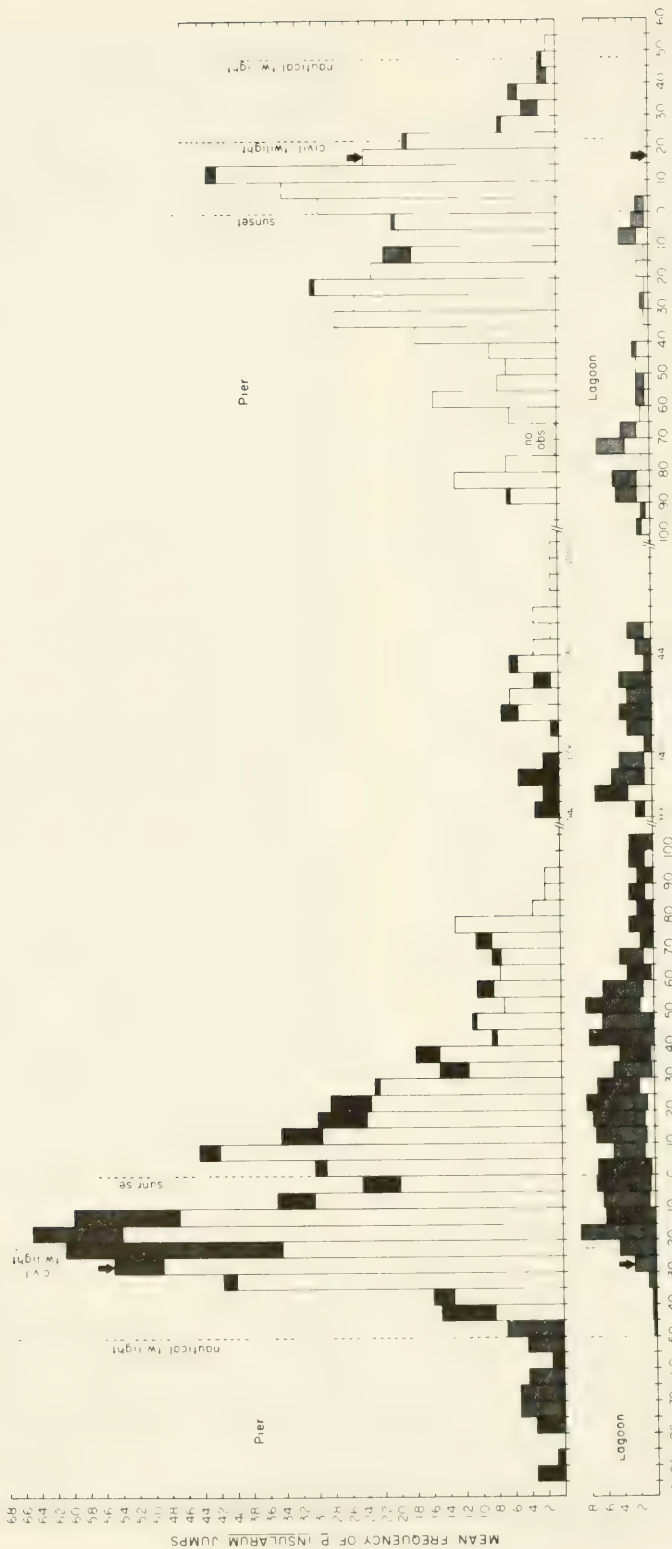

FIGURE 1.—Mean frequency of jumps (predator attacks) recorded for *Pranesus insularum* at 5-min intervals for Lalipuna Pier and HIMB lagoon areas. Times are presented relative to sunrise or sunset. Midday frequencies are presented with respect to local (real) time. The mean times of school formation in the morning and school breakup in the evening are denoted by the inverted arrows. Shaded bars denote deepwater (channel) jumps. Light bars denote shallowwater (reef) jumps. Double oblique slashes denote the breaks between morning, midday, and evening observations.

TABLE 2.—Comparison of school formation and breakup in *Pranesus insularum* with twilight phenomena recorded near Lilipuna Pier and HIMB lagoon, Kaneohe Bay, Hawaii.[1]

[Mean school formation = −29.4 min (before sunrise), mean school breakup = +19.1 min (after sunrise).]

Location	Date	Local time of sunrise (h)	Relative time of sunrise	Difference in time (minutes) between sunrise and: Beginning nautical twilight	Beginning civil twilight	Initial school formation	Schools formed
Lilipuna Pier	7 Oct. 1972	0625	0	−48	−23	−44	33
HIMB lagoon	8 Oct. 1972	0624	0	47	−22	−34	−24
	23 Oct. 1972	0629	0	−48	−22	−26	20
	19 Nov. 1972	0644	0	−51	−24	−38	31
	21 Nov. 1972	0646	0	−51	−24	33	28
	22 Nov. 1972	0647	0	−51	24	40	33
	12 Sept. 1973	0617	0	−48	−21	−24	−18
	14 Sept. 1973	0619	0	−48	−21	−23	21

Location	Date	Local time of sunset (h)	Relative time of sunset	Difference in time (minutes) between sunset and: End of nautical twilight	End of civil twilight	Initial school breakup	Complete school breakup
HIMB lagoon	8 Oct. 1972	1814	0	+48	+22	—	+26
	22 Oct. 1972	1804	0	+48	+22	+16	—
	13 Sept. 1973	1835	0	+48	+22	—	+24
	17 Sept. 1973	1832	0	+48	+22	+15	+21
	18 Sept. 1973	1932	0	+48	+21	+14	+18

[1]One-way ANOVA comparison of times of starting to school/schooling and starting to break up/complete breakup ($P = 0.004$)

Midday (1000-1500 H, Local Time)

In the pier area accurate counts of jumps made by the silversides during the time between 1000 and 1500 h local time were usually difficult to make due to waves caused by wind and nearby vessel activity.

Figure 1 presents the data collected during representative midday periods near the pier when interference was minimal. Generally, the silversides formed large elongated schools (hundreds to thousands of individuals) under or near the pier. The schools were largely inactive except when predators or potential predators such as barracuda, lizardfish, jacks, and needlefish, approached or attacked. When the tide level was low, the schools condensed and moved into deeper water near or under the end of the pier.

In the lagoon area at HIMB, the behavior and distribution of silversides was much the same during midday as it was near the pier (Figure 1). Small schools of silversides were strung out along the sides of the channel. Large schools of hundreds to thousands of fish were relatively inactive and concentrated over deeper water in the center of the lagoon. Barracuda and jacks were the most frequent predators, but lizardfish and leatherjackets were occasionally active in the lagoon.

Evening Twilight

As sunset approached, predator-prey activity increased in frequency in the pier area (Figure 1). Peak activity occurred between sunset and the end of the period of civil twilight and then declined rapidly to stop just after the end of the nautical twilight period. The silversides moved off the reef along, but in the direction opposite to, the path taken during the morning twilight movement onto and across the reef. Attacks and jumping occurred near the pier, then out over the reef, moved eastward along and parallel to shore, finally northward to the edge of the reef at the easternmost end of the observation area. As darkness increased, attacks and jumping gradually diminished in frequency and intensity (fewer individuals in smaller and fewer schools jumped).

In the lagoon area midday jumping activity in shallow and deep water continued until just after sunset, then stopped abruptly (Figure 1). The low number of jumps in deep water in the late afternoon and evening in the lagoon contrasts sharply with the frequency of jumps in the early morning (Figure 1). This difference may be related to the low levels of incident light striking the surface of the lagoon in the afternoon and evening due to the vegetation and the mountains and clouds to the northwest obscuring the sun. In the morning the lack of high vegetation and mountains nearby to the northeast resulted in light striking the lagoon's surface so that the silverside were presumably visible to their predators.

Light meter readings of 0.035-0.402 foot candle (Table 1) were made during the time (20-24 min

after sunset, i.e., during civil twilight) silverside schools were breaking up, the individuals spreading out just under the surface of the water. In 1972 and 1973 schools began to break up (increased interfish distances became noticeable) between 14 and 16 min after sunset and were spread out by 18-26 min after sunset (Table 2).

In summary, with the approach of dusk, predator attacks and silverside jumping increased in frequency and intensity to peak during the period of civil twilight, shortly after sunset, near the pier. In the lagoon there was no peak activity; the last attacks and jumps were recorded immediately after sunset. Peak jumping near the pier was recorded 5-15 min after sunset, just before the time the silverside schools were observed to break up becoming less polarized and cohesive (14-26 min after sunset, mean 19.1). In the lagoon, however, attacks stopped before the prey schools spread out; this may have been due to the shadows and increased darkness caused by heavy vegetation along the northwest side of the lagoon.

Silverside Behavior: Conclusions

The temporal pattern of predatory attacks and silverside jumping relative to sunrise was the mirror image of that relative to sunset, at least for the Lilipuna Pier area (Figures 1, 2). For each of the four environmental situations studied, Figure 2 simplifies and graphically presents (at 50-min intervals) the mean frequency of silverside jumps illustrated in Figure 1. Midday (1000-1500 h) jumps were combined and were not divided into 50-min intervals. Statistical comparisons (analysis of variance, $P \leq 0.05$) of the jumping data for sunrise (−50 to +50 min), midday, and sunset (−50 to +50 min) for each of the four situations indicated that, at least for the shallow-water reef area near Lilipuna Pier, the frequencies of jumps at sunrise and sunset were similar and differed from the number during midday.

The mean time of school formation occurred just prior to the beginning of civil twilight in the morning, and the mean time of the breakup of schools occurred just before the end of civil twilight in the evening. Peak predator activity occurred just after schools formed (mean time) in the morning and just prior to their breakup (mean time) in the evening. The data presented indicate that related events (e.g., school formation versus breakup) occurred in the study sites significantly

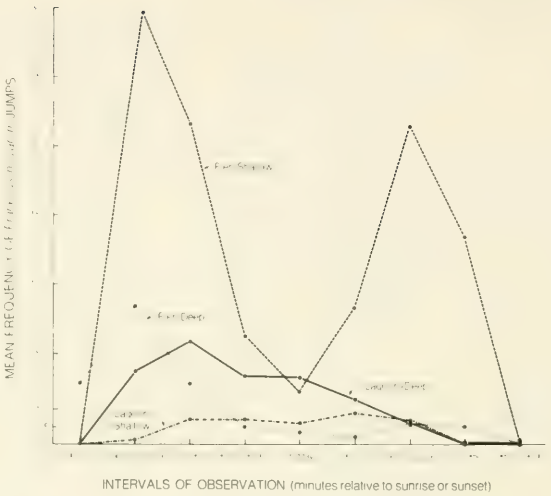

FIGURE 2.—Mean frequency of *Pranesus insularum* jumps for nine 50-min intervals (except midday). Based on data also presented in Figure 1.

earlier (about 5-15 min) in the evening, relative to sunset compared with the morning events, relative to sunrise (Table 2). This discrepancy may be due to the shadow effect of the clouds and mountains near Kaneohe Bay, which produce evening twilight conditions 5-15 min earlier than predicted, as discussed above. The relatively low frequency of deepwater attacks near the pier in the evening indicated that by the time silversides had moved off the reef and/or spread out, it may have been too dark for predators to see individual silversides. In the morning, the lack of mountains and vegetation and increasing light levels resulted in sufficient light being available for predators to see their prey.

Observations of free-living and particularly captive silversides, as well as my observations of other schooling prey species (striped mullet, *Mugil cephalus*, and Hawaiian anchovy, *Stolephorus purpureus*) in Hawaii, indicate that predation is of prime importance in shaping the behavioral patterns of prey species. When held captive in the absence of predators for days or weeks, individual prey in schools increased their interfish distances and appeared to feed more actively than they did in the field. When predators were present, interfish distances within captive schools were similar to interfish distances between individuals in the field. During the day, schooling behavior appears to serve a protective function for individuals, reducing the number of

attacks made by predatory fish. This protective function has also been observed for other schooling prey species (Radakov 1958, 1973; Neill and Cullen 1974). The chance that a predator has of singling out a specific individual silverside are greatly reduced if schools are formed. This appears to be especially true when the prey are polarized towards one another and move close together through coordinated maneuvers. In the field, when predators were not in the immediate vicinity of silverside schools, individual silversides became relatively motionless and randomly oriented towards one another, darting out from schools presumably to feed. When individual silversides presumably became exposed and/or appeared to be accessible to one or more nearby predators, the predators approached or attacked. If the predator's approach was slow, the individual silversides became polarized, the school maneuvering evasively. If a predator's approach was sudden or rapid, individual silversides jumped out of the water one or more times to evade. Both schooling and jumping presumably decrease the time a predator had to align itself with a specific individual prey. In addition, a jumping silverside often landed in the midst of its own, or that of another nearby, school, presumably disappearing from the predator's field of vision and/or path of swimming. The formation of large schools composed of many hundreds or thousands of individuals, especially a number of such schools relatively close to one another, appeared to increase an individual silverside's chance of escape when jumping.

The movement of silversides into the shallow water over reefs, and their location near and under Lilipuna Pier and heavy overhanging vegetation and along the sides of the lagoon, may be additional means, besides schooling, of reducing predation. In the shallow water near the pier, the most common vertical attacking predators were lizardfish. In deeper water in the lagoon and near the pier, jacks and leatherjackets also attacked vertically. Horizontal stalking and attacking predators, such as barracuda and needlefish, occurred in both deep and shallow water. The depth of water over the reefs may have been less than sufficient for some of the vertical attacking species to maneuver and approach schools of silversides undetected. The occurrence of silversides near structures and along the sides of the lagoon may have also limited the maneuverability and avenues of approach for all species of predators.

DISCUSSION

The interactions between silversides and their predators in relation to solar phenomena are almost identical in pattern and time to those given by Hobson (1968, 1972) for the interactions of *Harengula thrissina* and their predator *Mycteroperca rosacea* in the Gulf of California. Hobson and Chess's (1973) study of the arrival and departure of *Pranesus pinguis* to and from reefs at Majuro Atoll in the Marshall Islands also showed school movement related to specific times during twilight. However, only a few predatory attacks were observed at Majuro Atoll. Comparisons of lunar and tidal changes during the studies in Kaneohe Bay and Majuro Atoll and Baja California seem to indicate a relatively minor influence on the crepuscular behavior of schools.

Hobson (1968, 1972, 1973), Collette and Talbot (1972), and Domm and Domm (1973) have demonstrated that there is relatively little activity amongst most coral reef fishes during a specific segment of the twilight period. In the morning, nocturnally active reef fish leave the open water column to hide in the coral reef approximately 30 min before sunrise (Hobson 1972). Diurnal species do not reoccupy the water column until approximately 12-16 min prior to sunrise. It is exactly between the above times, the "quiet period," as defined by Hobson (1972), that peak surface predator-prey activity and school formation takes place in Kaneohe Bay, just as it does in the Gulf of California (Hobson 1968, 1972), and possibly Majuro Atoll (Hobson and Chess 1973). The pattern is reversed during evening twilight (Hobson 1972). Diurnal reef species evacuate the water column approximately 6-22 min after sunset. Nocturnal species then reoccupy the water column about 14-34 min after sunset. Again, surface predator-prey interactions peak and schools break up in Kaneohe Bay during the time that would be comparable with the evening quiet period in other parts of the world.

The combined observations of reef fishes in the Virgin Islands (Collette and Talbot 1972), the Great Barrier Reef, Australia (Domm and Domm 1973), Hawaii (Hobson 1972), and the Gulf of California (Hobson 1968) indicate nearly identical time relationships of behavioral events during

the twilight transitional periods. This would be the predicted relationship since fish respond to specific intensities and spectral composition of light (Munz and McFarland 1973). The intensity and spectral composition of incident light at specific times relative to sunrise or sunset are identical each day, although they vary with time and season and with latitude. The amount of cloud cover and/or high mountainous terrain nearby, as in Kaneohe Bay and Kona, Hawaii (Hobson 1972) or Baja California (Hobson 1968), may shift the activity patterns to later in the morning, or earlier in the evening (i.e., shift the time relative to sunrise and/or sunset at which specific light levels occur). However, the basic relationships between behavior and twilight periods appear to hold.

Light meter readings recorded during the formation and break up of Hawaiian silverside schools are compared with those recorded for two other species of siversides in Table 1. The readings for all three species are not significantly different. Such light levels occur naturally when the sun is between $-5°$ and $-9°$ below the horizon during the periods of evening or morning twilight (Brown 1952). These data and the field observations reported here are also comparable to the light levels and the sun angles calculated from the data presented by Pavlov (1962) for another silverside, *Atherina mochon pontica*. Pavlov found that peak predator success occurred at light levels of approximately 0.01-108 foot candles corresponding to sun angles of $-9°$ to $+1°$ to the horizon (Brown 1952) (i.e., centered during the period of civil twilight).

These comparisons indicate that related species of silversides, which live in widely separate parts of the world, have similar visual thresholds and, perhaps, sensitivity. Munz and McFarland (1973) provided a synopsis of research, which has shown that many related species demonstrate a considerable diversity in their visual sensitivity. However, species, whether related or not, which occur in similar environments, appear to have similar thresholds and sensitivity. These relationships indicate that the above silverside species from various locations in the world may have very similar behavioral patterns and/or live in very similar physical and biological environments.

When light levels decrease in the evening, visual thresholds may be reached, making coordinated schooling movements impossible, or at least more difficult for the silversides. These thresholds may be reached at the time when cone vision shifts to rod vision (the Purkinje shift), neither cone nor rod vision being fully efficient (Munz and McFarland 1973). As school formation breaks down or increases, the silversides appear to be the most vulnerable to predatory attack. This vulnerability may be due to reduced visual sensitivity, leading to an inability to see their predators below them against a dark bottom or deep water (Hobson 1966, 1968) and react in time to avoid and escape from them (Dill 1972, 1974a, b). In addition, such prey may be unable to simultaneously interact with conspecifics, and look out for predators at a distance at low light levels.

Predators are presumably able to see their prey at a horizontal angle or silhouetted against the twilight sky for a short period of time before their lower visual threshold is reached in the evening (Hobson 1966, 1968). Munz and McFarland (1973) indicated that increased visual sensitivity in predators, which provides sufficient resolution for the detection of prey in motion during twilight, may be a result of having relatively larger, but fewer, cones in their retinas compared with those found in diurnal fishes. This factor is critical since predators must align themselves and be able to predict where their prey will be during the mouth opening phase of their strike (Nyberg 1971).

Weighing against the hypothesis that the schools of silversides break up and reform as a result of changes in visual sensitivity, are a number of observations made of captives held in the field enclosures in the absence of predators. When held for weeks at a time, these silversides did not completely lose their cohesion and polarity, indicating that there may be a strong genetic component to their schooling behavior. This genetic component may result in the silversides remaining within a short distance of one another at all times. The silversides appear to be adapted to feeding at night as well as in the day (McMahon 1975). If they can feed at night, the silverside are probably able to detect the presence of conspecifics, either using visual and/or lateral line cues. The ability to detect conspecifics would be particularly beneficial as individuals would not become so widely scattered during the night that polarized schools could not easily reform during morning twilight. In addition, the observation that captive silversides held in large enclosures in the field in the absence of predators did not all spread out to look continuously for food indicates

that there may be a biological (circadian) rhythm related to school formation and breakup and the availability of specific food resources. Thus, the breakup of schools may reflect a preemptory predilection of individual silversides to spread out and feed rather than remain within the safety of compact polarized schools. Concurrently, predators are rapidly losing their ability to distinguish individual silversides in the fading light, but their presence remains a threat.

During the morning the process is reversed as light levels increase with predators becoming increasingly active and presumably more successful at capturing silversides. It is during relatively short daily time spans within the periods of twilight that the silversides become particularly vulnerable to certain predators. It is at these times that the silversides are passing to or from a period of feeding to a period of relative quiescence. In some areas, exposure to predators may be increased because the transition involves the movement from one location to another. The timing of such movements and the behavioral changes that occur within schools appear to be related to the threat of predation, the availability of food and the visual sensitivity and thresholds of both the silversides and their predators.

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FISHES, MACROINVERTEBRATES, AND THEIR ECOLOGICAL INTERRELATIONSHIPS WITH A CALICO SCALLOP BED OFF NORTH CAROLINA

FRANK J. SCHWARTZ AND HUGH J. PORTER[1]

ABSTRACT

A 1972 study documented the fishery, fish and macroinvertebrate faunas, possible predators, and the ecological interrelationships of the offshore North Carolina calico scallop, *Argopecten gibbus,* bed(s). Environmental data of water temperature, salinities, chlorophyll a, water current direction, sediment grain size, and organic composition were obtained aboard commercial and chartered research vessels. Water temperatures progressed seasonally from 12° to 26° C while bottom salinities varied between 31 and 37‰ yet were not radically different from the surrounding habitats. Chlorophyll a data suggested a fairly stable but low plankton fauna over the bed(s) except for June and late October. Little or no differences in bottom type within or without the bed(s) were noted on the basis of sediment particle size, grain size, skewness, or sorting coefficients. Scallops grew faster in the experimental bed than in the commercial bed but little could be found to account for their differences in size. Some 111 species of fishes were captured over the bed(s). Of a vast moving fish fauna, 33 species dominated the catches. Of 46 species with food in their stomachs, 20.4% feed on scallops with only 9 species considered scallop predators. Bothids, soleids, rajids, labrids, dasyatids, and myliobatids were not active scallop predators. *Halichoeres caudalis* appeared in October when the fishery collapsed economically. Of 12 species of echinoderms, the sea stars *Luidia clathrata* and *Astropecten articulatus* were active scallop predators. While less abundant, 21 additional invertebrates were also suspected predators. *Luidia clathrata* and *A. articulatus* abundance on the beds remained high throughout the season; however, abundance off the beds was somewhat lower. No one factor has yet been found that made the North Carolina calico scallop beds unique, why they existed, or were productive in 1972.

Three commercial species of scallops occur in North Carolina: the Atlantic deepwater scallop, *Placopecten magellanicus* (Gmelin), the shallower offshore calico scallop, *Argopecten gibbus* (Linné), and the inshore bay scallop, *Argopecten irradians* (Lamarck). The offshore calico scallop fishery, while yielding varying quantities of harvestable scallops (Table 1), has alternately experienced good and bad years of production (Lyles 1969; Cummins 1971; Chestnut and Davis 1975). The disappearance of calico scallops from an area, whether off North Carolina, Florida, or elsewhere, is common knowledge (Bullis and Ingle 1959; Hulings 1961; Anonymous 1962; Kirby-Smith 1970; Roe et al. 1971; Porter and Wolfe 1972). Off North Carolina the causes of scallop fluctuations and production have been attributed to mortalities, migration, poor larval transport from elsewhere, introduction of scallop shucking and eviscerating machines, or overfishing (Webb and Thomas 1968; Lyles 1969; Cummins and Rivers 1970; Kirby-Smith 1970; Cummins 1971; Allen and Costello 1972). This report documents the fish and macroinvertebrate faunas, possible predators, and their ecological interrelationships with the scallop bed(s) that supported the 1972 fishery.

TABLE 1.—North Carolina calico scallop production, 1959-75.[1]
[No production 1962-64, 1968-69, and 1974-75.]

Year	Meats (pounds)	Value (dollars)	Gear
1959	6,572	2,629	Dredge
1960	111,726	44,691	Trawl
1961	22,427	8,971	Trawl
1965	871,100	244,709	Trawl
1966	1,856,760	368,685	Trawl
1967	1,388,606	308,843	Trawl
1970	1,574,087	498,570	Trawl
1971	1,285,304	432,025	Trawl
1972	1,050,320	492,899	Trawl
1973	556,315	353,757	Trawl

[1]Data supplied by the National Marine Fisheries Service Statistical Office, Beaufort, N.C., and Chestnut and Davis 1975.

NORTH CAROLINA CALICO SCALLOP FISHERY

While *A. gibbus* occurs in the western North Atlantic from the northern side of the Greater Antilles and throughout the Gulf of Mexico to

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Bermuda and possibly Delaware Bay (Waller 1969; Allen and Costello 1972), only three areas produce calico scallops of commercially harvestable quantities: North Carolina, Cape Canaveral off eastern Florida, and the Gulf of Mexico off Apalachicola Bay, Fla. (Drummond 1969; Cummins 1971; E. Willis pers. commun.). Throughout its range it has been found in depths of 2-370 m (Waller 1969). Off North Carolina, calico scallops occur at open water depths of 13-94 m (Cummins et al. 1962; Bullis and Thompson 1965; Porter 1971, 1972a; Allen and Costello 1972).

Until recently, North Carolina calico scallops were hand shucked by shore-based operations (Cummins 1971). In 1970, two shucking machines (Webb and Thomas 1968) were introduced in North Carolina and by 1975 there were eight. The present North Carolina and Florida fisheries prefer this shucking method rather than utilizing offshore vessels equipped with machine shuckers, as was briefly used off Florida (Allen and Costello 1972). Generally, commercial fishing is considered feasible when 20 bushels (in shell) are caught per hour with shell diameter of at least 40 mm (Drummond 1969). Meat size to be acceptable to hand shucking should be 190 meats/kg or 90 meats/pound (Cummins 1971). Machine processed meats can be as small as 495 meats/kg (225 meats/pound).

Off North Carolina, the high cost of hand shucking and the early lack of knowledge concerning a possible calico scallop fishery delayed its development (Chestnut 1951). The fishery seems to have begun in 1959 and has since been described by Cummins et al. (1962), Cummins (1971), Porter (1971, 1972a), and Porter and Wolfe (1972). At first scallop dredges were used to harvest calico scallops. Today, otter trawls are the gear used by the commercial fishery (Rivers 1962). Short tows of 10-15 min often land 60 or more bushels, with an average day's catch being 800-1,500 bushels of shell stock.

STUDY AREA

Cummins et al. (1962) characterized the principal North Carolina calico scallop grounds as an elliptical shaped bed 16 km long near Cape Lookout, with several lesser beds located in 19-37 m depths northeast and southeast of the Cape. The major North Carolina calico scallop fishery in 1971 was located southeast of Cape Lookout; a small bed southeast of the Cape was also fished briefly in September of that year. Exploratory efforts in 1972 by the commercial fleet and the RV *Dan Moore* on the beds southwest of New River and northeast of Cape Lookout (Figure 1) failed to locate commercial quantities of calico scallops. The only beds that supported the 1972 fleet of 13 vessels from February to October were located 16-24 km south of Beaufort, N.C., producing some 1 million pounds of meats (Table 2).

The 1972 study area consisted of the above beds located at lat. 33°35′N between long. 76°35′ and 76°55′W (Figure 2). Depths were 20-25 m and most sampling occurred inside the 28-m contour.

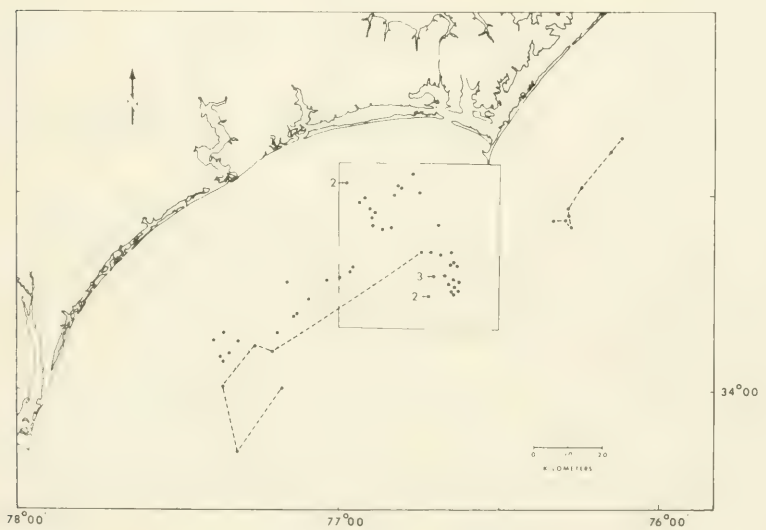

FIGURE 1.—North Carolina calico scallop fishing grounds. Dots refer to areas of poor catch by commercial fishermen during the 1972 season. Dashed lines indicate exploratory trips by one or more trawlers. Solid line refers to the area contained in Figure 2. Dotted line indicates 20-fathom (36.6-m) contour.

TABLE 2.—North Carolina calico scallop production, 1972.[1]
[No production in November and December.]

Month	Pounds	Value ($)	Month	Pounds	Value ($)
Jan.	2,800	1,624	July	68,768	46,763
Feb	24,064	9,626	Aug.	43,624	35,772
Mar.	184,688	72,028	Sept.	33,008	29,047
Apr.	280,800	101,087	Oct.	544	478
May	228,400	93,644	Total	1,050,320	492,899
June	183,624	102,830			

[1]Data supplied by the National Marine Fisheries Service Statistical Office, Beaufort, N.C., and Chestnut and Davis 1975.

METHODS

Sampling Vessels

Two types of vessels were used to sample the offshore North Carolina calico scallop beds. Commercial fishing vessels, from which most of the samples were obtained, were the 25-m MV *Ensign,* a side trawler of Gloucester design and the 15-m MV *Seven Brothers,* a double rigged shrimper design. Research vessels include the RV *Beveridge,* a 17-m shrimp trawler which was chartered monthly to collect additional samples or to maintain anchored equipment, and the Duke University 33-m RV *Eastward,* a side trawler of Gloucester design. One bottom observational cruise was accomplished by using RUFAS (Anonymous 1969) aboard NOAA RV *George M. Bowers.* Two additional samples, 23 April and 27 June, were also obtained while returning from other *Eastward* projects.

All commercial or chartered vessels towed one or two 10-12 m scallop trawls (Rivers 1962) which were modified to have heavily weighted foot lines and heavy-duty chaff gear on the cod end. The trawl on the *Beveridge* was rigged the same as that of the commercial vessels except that the foot line was the standard weighted loop chain design preceded by a light tickler chain. Mesh size of all trawls was the standard flat shrimp type. Sampling tow interval varied on the commercial vessels by season as a function of scallop abundance. *Beveridge* or *Eastward* tows were kept to 15 min. Sample tow distances, by commercial vessels, varied ¼-½ km, whereas *Beveridge* and *Eastward* tows were ¼ km. No effort, by type of vessel, was made to sample with or against the current.

Environmental Data

Water temperatures were obtained with a mercury thermometer immersed in bottom water obtained by a 3.1-liter Kemmerer sampler.

Salinities were determined from the water sample by using a direct reading American Optical Corp.[2] refractiometer.

Chlorophyll a was determined spectrophotometrically for 19 stations (Figure 2) following the methods of Strickland and Parsons (1968) and expressed as milligrams per cubic meter.

A Braincon 381 current meter was anchored and buoyed at the northwestern edge of the commercial grounds. Excessive fouling during much of the sample year by hydroids, sponges, and tunicates prevented precise long-term bottom current data being recorded at the surface of the bed. After rebouying the meter to record currents 30 cm above the bed, current data obtained over a 26-day period, mid-August to mid-September, indicated a northeastward current drift component (Schumacker 1974).

Sediment samples taken by Peterson (*Beveridge*) and Shipek (*Eastward*) grabs (Figure 3) were frozen until grain size and organic determinations could be made. Pretreatment for grain-size analysis included washing each sample in a large volume of fresh water and then decanting after all sediment had settled. Washing was done to reduce weighing errors induced by salt crystals. Following decanting, sediments were oven dried at 85°C and separated into sediment sizes by a U.S. Standard Sieve Series and mechanical sieve shaker. All samples were in the shaker for at least 2 h. Analysis of data followed Morgans (1956).

Percent organic material was determined from 1 to 2 g unwashed subsamples which had been oven dried for 48 h at 85°C. The amount of organics was assumed to be the difference in sample weights before and after firing at 500°C for 2 h. This followed a technique used in the Marine Sediments Laboratories of Oregon State University (J. Paul Dauphin pers. commun.).

An attempt was made to develop a fast method for percent organic determinations of marine sediments through the manufacturer's suggested use of a Coleman Model 33 Carbon-Hydrogen Analyzer, rented from the Duke University Marine Laboratory. Comparison of data, by statistical means, showed no correlation between analyzer and ovenfired organic values from offshore marine sediments.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

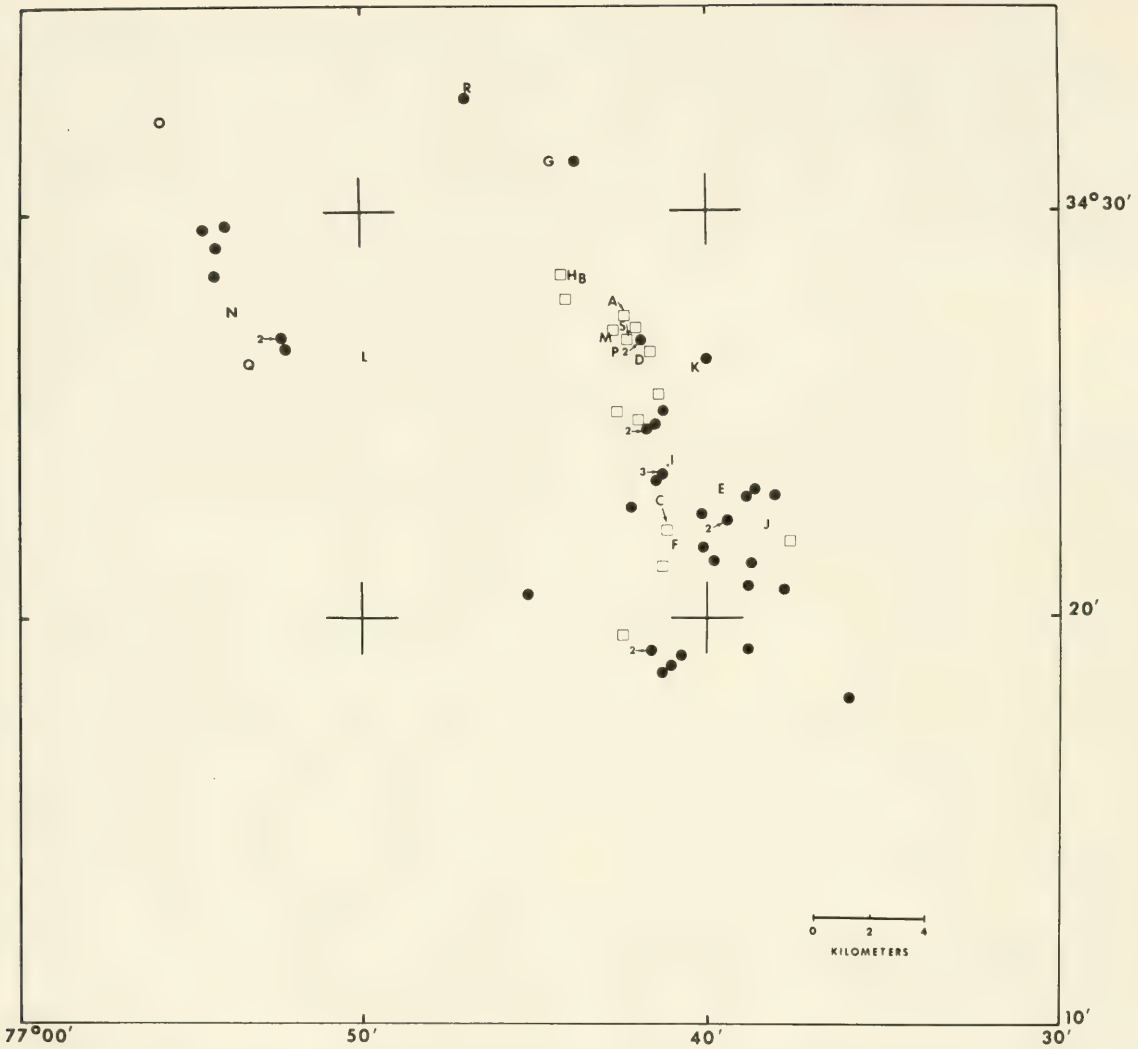

FIGURE 2.—North Carolina calico scallop fishing grounds. Dots refer to known locations of good catches by commercial trawlers. Open squares refer to known locations of good catch by RV *Beveridge*. Letters refer to chlorophyll a sampling stations. For location of enclosed area off North Carolina coast see Figure 1.

Fishes

Fishes of at least 100 mm standard length were tagged using 12-mm Peterson disk tags held in place (in the middorsolateral musculature) by Monel pins. Fish lengths, except for skates and stingrays where wing width was used, were expressed for each species and specimen as standard length. Once tagged, release was immediate over the original collecting site. The ship's loran was used to pinpoint the release site. Other biological data were taken on those additional fishes that had not been too badly damaged by the fishery or scallop catches. Notations of other fishes not captured, such as flyingfishes, completed the field data.

Fish samples from commercial catches and destined for stomach content analyses were kept on ice because of the danger of Formalin contamination of the scallop catch and the cramped ship quarters prevented carrying extra gear afield. Similar fish sampled aboard research vessels were preserved in 20% Formalin. In the laboratory, the entire digestive tract was removed, contents identified, and noted whether the food items were in the stomach or intestine. Positive identification of

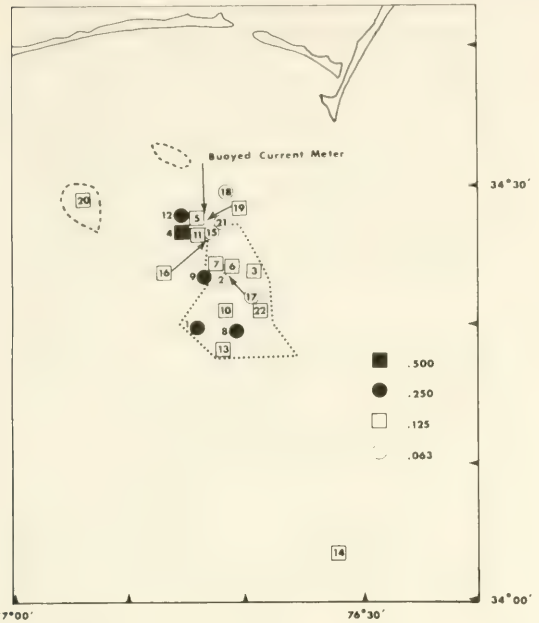

FIGURE 3.—Twenty-two sediment sample stations. Dominant grain size is indicated by station. Broken lines enclose the commercial area, an area fished by the calico scallop fishery.

the food items to species was possible in most cases.

Scallops

Scallops were sampled from two areas—one general and one specific. The general area, hereafter referred to as the commercial area, included wherever the scallop fishery was operating (Figures 1-4). Scallop tissue samples from this area were taken, when possible, once a week; shell length measurements and other appropriate scallop data were taken more frequently. Tissue, gonad and/or spawning condition data will be covered in a paper by Porter and Schwartz (in prep.).

The specific area, hereafter referred to as the experimental area, was an area just northwest of the commercial area. This area was sampled monthly by the *Beveridge* and was marked from June to September 1972 by a large red buoy; this buoy further served to support the Braincon current meter (Figure 3). The seabed interval between this area and the commercial area to the south contained no scallops, which suggested that this area was a small separate bed. Only briefly during the latter part of the commercial scallop season was the experimental area worked by the 1972 fishery.

Sea Stars

Data were accumulated on seasonal distribution of the sea stars present on the scallop beds, their size, and relative abundance. Sea star size is here defined as the radius of a sea star through its longest arm.

About 20 *Astropecten articulatus* and about 20 *Luidia clathrata* were examined weekly, when available, for stomach contents. *Luidia alternata, Goniaster americanus,* and *Echinaster brasiliensis* stomachs were also examined, when available. Stomach analysis examinations which also delineated associated organisms were similar to those of Porter (1972b) and will be reported on elsewhere.

Associated Macroinvertebrates

Unculled bushels of scallops, as caught by the trawlers, were examined periodically by the field investigator to note other associated organisms, amount of shell material, and signs of dead or dying scallops. Counts were made of each organism and the amount of dead shell or trash. A log was also kept of all macroinvertebrate species seen during each cruise.

ENVIRONMENTAL OBSERVATIONS

Bottom water temperatures exhibited a natural progression from about 12°C in February to a high near 26°C in September. These were within the range 9.9°-33°C noted by Waller (1969). Vernberg and Vernberg (1970), in laboratory experiments of North Carolina calico scallops, found none survived after 48 h exposure to water of 10°C.

Bottom salinities throughout the bed, as evidenced during the shifting seasonal fishing effort (Figure 4), remained fairly constant at 35‰ (range 31-37‰, Figure 5). This agreed with observations of others for scallop grounds elsewhere (Anderson et al. 1961; Hulings 1961; Grassle 1967; Pequegnat and Pequegnat[3]).

Kirby-Smith (1970) and Allen and Costello (1972) suggested that upwelling in the vicinity of

[3]Pequegnat, W. E., and L. H. Pequegnat. 1968. Ecological aspects of marine fouling in the northeastern Gulf of Mexico. Texas A&M Univ. Dep. Oceanogr. Proj. 286-F, Ref. 68-22T, 80 p.

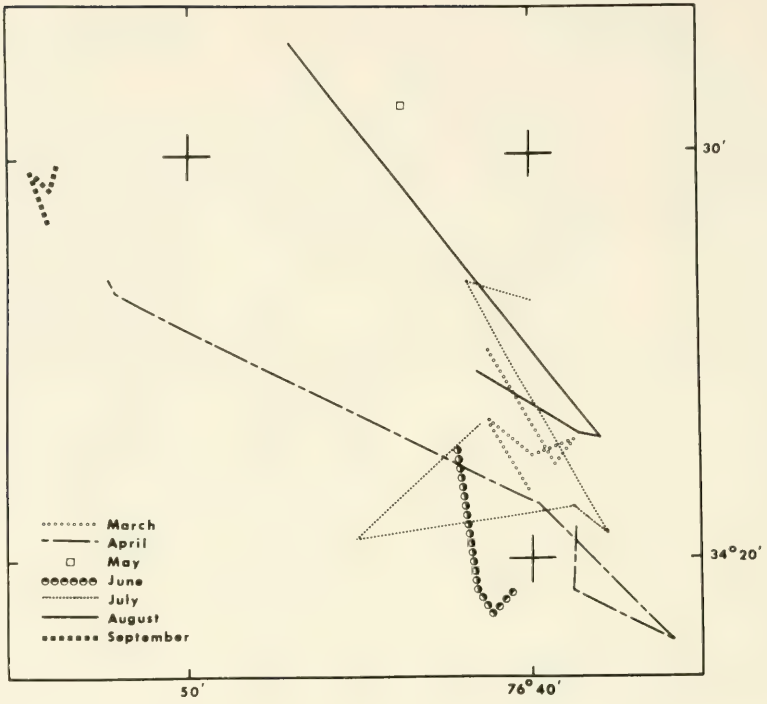

FIGURE 4.—Areas fished by commercial fishery during the 1972 season. Locations taken from ship's log.

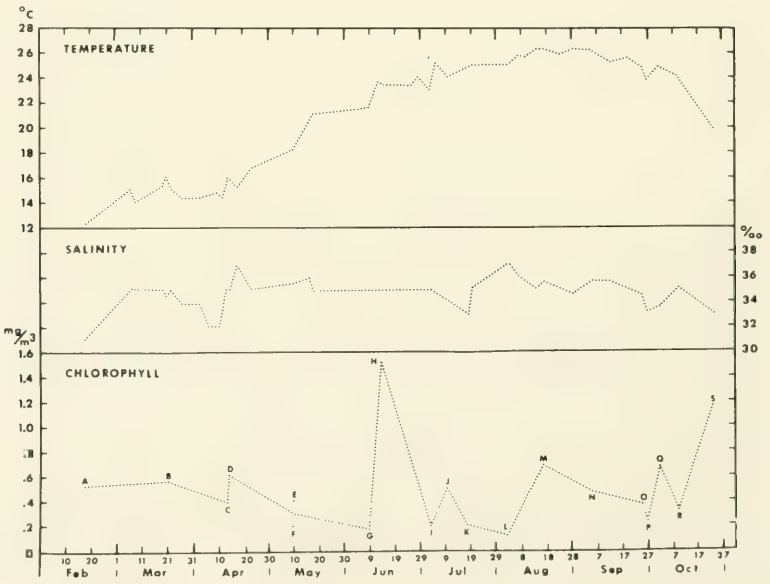

FIGURE 5.—Environmental data collected from the calico scallop grounds. Each data point for water and salinity indicates individual date sampled. Letters on chlorophyll graph refer to station sampled that date, see Figure 2 for locations.

Cape Lookout (Taylor and Stewart 1959; Wells and Gray 1960; Gaul et al.[4]) may produce high plankton concentrations and that these concentrations may occur where scallop abundance is greatest. Chlorophyll a analyses during 1972 (Anonymous[5]) suggested that a fairly stable but

[4]Gaul, R. D., R. E. Boykin, and D.E. Letzring. 1966. Northeast Gulf of Mexico hydrographic survey data collected in 1965. Texas A&M Univ. Dep. Oceanogr. Proj. 286-D, Ref. 66-8T, 202 p.

[5]Anonymous. 1972. Data report for R/V *Eastward* cruise E-12-72, July 3-8, 1972. Duke Univ. Mar. Lab., Beaufort, N.C., 34 p.

low plankton fauna existed over the scallop beds, except during June and late October, when indications of a late spring and early fall bloom occurred (Figure 5).

Twenty-two sediment samples were taken during the 1972 study (Figure 3). Of these, seven were deliberately taken in areas where no scallops were collected by the fishery (Table 3). As the sediments were taken immediately after a trawl tow, they may not be representative of the same bottom covered during the tow. No discernible differences were found between sediments from scallop producing and nonproducing areas (Table 3, Figure 2).

Newton et al. (1971, Sediment Distribution Chart No. 2) characterized the area which was later encompassed by the 1972 commercial scallop fishery (Figures 3, 4) as consisting of two sediment

TABLE 3.—Sediment size analyses, data listed as percent per sample, sediment sorting coefficients, skewness, for scallops sampled in 1972 from producing and nonproducing areas off North Carolina.

Sediment size (mm)	Sediment sample station and sample date						
	1	2		3	4	5	6	7
	18 Feb	18 Feb		18 Feb.	18 Feb	21 Mar	21 Mar.	21 Mar
>4	0.572	0.701	1.031	0.102		0.072	0.406	0.0027
2-4	1.734	0.381	0.626	0.165	18.235	0.362	0.381	0.0068
1-2	8.289	1.530	2.715	0.573	22.831	0.651	0.964	0.0139
0.5-1	32.299	2.325	3.903	2.090	25.053	1.505	2.224	0.0303
0.250-0.5	40.606	3.898	5.842	34.711	19.814	13.576	12.670	0.1443
0.125-0.250	13.847	14.748	14.649	49.834	7.782	81.622	40.021	0.2982
0.063-0.125	1.826	69.186	64.396	9.836	3.431	0.001	40.096	0.4646
<0.063	0.826	7.231	6.837	2.688	2.855	2.211	3.239	0.0392
Median particle size[1]	1.17	3.37	3.32	2.22	0.35	2.42	2.80	3.02
Median particle size (mm)	0.44	0.09	0.09	0.21	0.77	0.17	0.14	0.12
Sediment sorting coef[1]	0.675	0.365	0.485	0.555	1.100	0.300	0.635	0.685
Sediment skewness[1]	−0.045	0.015	−0.105	−0.035	0	−0.020	0.035	−0.155
Percent organic	2.027	1.080		0.844	2.118	0.884	0.790	1.394
Latitude N	34°22′	34°24′		34°24′	34°26.5′	34°27′	34°24′	34°24′
Longitude W	76°44′	76°42′		76°39′	76°45′	76°44′	76°41′	76°42.5′
Depth (m)	25	24		24	22	22	24	25
Scallop producing area	no	yes		no	yes	no	yes	yes

Sediment size (mm)	8	9	10	11		12	13	14
	21 Mar.	21 Mar.	10 May	14 June		14 June	14 June	25 June
>4	0.0019	0.0313		8.026	3.640	0.491	0.012	0.064
2-4	0.0196	0.0347	0.341	8.118	3.855	1.088	0.339	0.074
1-2	0.0595	0.0643	1.062	8.102	7.438	3.318	1.084	0.890
0.5-1	0.2356	0.2678	2.769	19.210	19.475	9.113	5.071	3.936
0.250-0.5	0.5574	0.4873	11.619	2.623	2.810	44.895	27.046	30.632
0.125-0.250	0.1132	0.0854	44.095	28.842	40.369	6.080	61.209	62.931
0.063-0.125	0.0096	0.0207	31.974	13.432	16.683	30.813	5.218	1.231
<0.063	0.0032	0.0085	8.139	11.647	5.730	4.201	0.022	0.242
Median particle size[1]	1.33	1.22	2.78	2.13	2.32	1.80	2.27	1.23
Median particle size (mm)	0.39	0.42	0.14	0.22	0.18	0.28	0.20	0.41
Sediment sorting coef[1]	0.525	0.645	0.650	1.465	1.215	1.060	0.505	0.480
Sediment skewness[1]	−0.085	−0.145	0.070	−0.615	−0.605	0.500	−0.095	−0.090
Percent organic	2.176	2.461	ND[2]	1.638		0.885	0.763	0.840
Latitude N	34°19.5′	34°23.5′	34°21′	34°27′		34°27.5′	34°18.5′	34°3.4′
Longitude W	76°41′	76°43.5′	76°41.5′	76°44′		76°45′	76°42′	76°32.7′
Depth (m)	28	23	26	23		21	29	37
Scallop producing area	yes	yes	yes	no		no	yes	no

Sediment size (mm)	15	16	17	18	19	20	21	22
	27 June	17 Aug	17 Aug.	17 Aug.	12 Sept.	12 Sept	23 Oct.	23 Oct
>4	1.082	0.021	0.044	0.000	0.049	0.000	0.665	0.243
2-4	1.016	0.437	0.146	0.234	0.363	0.001	0.480	0.446
1-2	1.472	1.556	0.756	0.603	1.043	0.007	1.386	1.162
0.5-1	2.573	3.345	2.472	2.646	2.103	0.026	2.515	2.821
0.250-0.5	5.800	24.389	6.758	8.376	6.175	0.209	6.451	11.387
0.125-0.250	14.705	58.881	20.293	23.028	62.728	0.638	20.518	46.534
0.063-0.125	66.049	9.525	62.619	59.094	26.885	0.097	62.462	35.038
<0.063	7.304	1.847	6.912	6.019	0.654	0.022	5.523	2.370
Median particle size[1]	3.35	2.36	3.32	3.26	2.65	2.38	3.27	2.72
Median particle size (mm)	0.09	0.19	0.10	0.10	0.15	0.19	0.10	0.15
Sediment sorting coef[1]	0.425	0.485	0.500	0.555	0.465	0.380	0.505	0.585
Sediment skewness[1]	−0.055	−0.075	−0.100	−0.135	0.065	0.020	−0.095	0.090
Percent organic	0.967	1.151	0.866	1.037	0.593	1.251	1.021	1.119
Latitude N	34°26.3′	34°26′	34°23.5′	34°29.5′	34°27′	34°29′	34°27′	34°21′
Longitude W	76°43′	76°43′	76°41′	76°41.5′	76°42.5′	76°54′	76°42′	76°38.5′
Depth (m)	18	22	23	19	21	20	21	26
Scallop producing area	yes?	yes	yes	no	yes?	yes	yes	yes

[1]See Morgans (1956) for definition
[2]Not determined

types, most of the bed being "fine sand - grey" while areas of its western edge were "shell hash - often brown - many types of organic contributors." The latter was typical of our sediment sample 14. The area from which sediment sample 20 was taken was characterized as "Coarse sand - very shelly - iron stained"; the experimental area northwest of the main scallop producing area was characterized as "fine sand - iron stained - less than 25% shell material." Median grain size analyses of our data agreed with Newton et al. (1971) in that parts of the western edge of the calico scallop bed had coarser sediments than other areas encompassed by the main bed (Figure 3); however, no differences were found between the main scalloping area, the experimental area north of the bed, and stations 14 and 20.

Sanders (1958) and Bloom et al. (1972) suggested that optimal sediment conditions for filter feeders were a fine (about 0.18 mm) and a well-sorted, but positively skewed, grain size. Median sediment sizes found within the 1972 North Carolina calico scallop bed averaged below Sanders' 0.18 mm optimal size for filter feeders. Subsequent to this study, plotting the location of the 1973 calico scallop fishery off the North Carolina coast on the Newton et al. (1971) sediment chart, revealed that the 1973 fishery was in an area not of fine sand but very coarse shelly sand. This has been further corroborated by personal observations aboard vessels in the fishery. These data may support the contention of McNulty et al. (1962) that other factors besides grain size are important to the well being of filter feeders.

Sorting coefficient values for most sediment samples ranged from 0.300 to 0.685 (Table 3, a condition considered well sorted), although two samples located northwest of the main fishery had relatively high sorting coefficients (1.100 to 1.465). Sediments in these same two samples were also strongly skewed (−0.615 and 0.500, Table 3). While sorting coefficient values agreed with the conclusions of Sanders (1958) and Bloom et al. (1972), the sediment skewness data did not. Most of the data was only slightly skewed (−0.155 to 0.090) and not strongly positively skewed as they suggested.

Commercial fishermen reported that there were numerous rough areas, including a small low ledge, outside the commercial area which caused great damage to their nets. Porter and Wolfe (1972) described the North Carolina scallop grounds as consisting of sand, shell fragments, and occasionally large pieces of trent marl and coquina. Porter and Wolfe (1972) and Pearse and Williams (1951) described a small bed southwest of New River which was surrounded by bottom containing large heads of lobe star coral, *Solenastrea hyades* (Dana). During 1972, large masses of trent marl were not infrequently brought up in the scallop nets by the commercial fishermen. Ledgelike outcroppings of marl (?) and large heads of the lobe star coral outside the commercial area were observed in 1972 while aboard the *George M. Bowers* through use of its remote underwater television sled RUFAS. While such marl outcrops and coral heads are not uncommon throughout the southern North Carolinian coastal area, known calico scallop beds do not seem to be dependent upon their presence.

CALICO SCALLOP GROWTH

Length measurements were taken on 5,180 scallops during the sampling period (Table 4). Scallop (865) mean growth in the experimental area was faster than that from the commercial area (Table 4); size increase over a 7-mo sampling period was 17.8 mm or 2.5 mm/mo. Comparable growth data obtained from 4,315 scallops landed by the commercial fishery over the 9-mo sampling period were 8.7 mm or 1.1 mm/mo; their sizes ranged from 35 to 65 mm with no live small scallops being noted. The difference in rate of growth was probably related to the original smaller size of the experimental area scallops, which ranged from 28 to 57 mm in length (Table 4). Allen and Costello (1972), reviewing the calico scallop literature, noted growth data of 4.0 mm/mo for scallops having mean sizes of 13.9 to 37.8 mm and 0.3 mm/mo for scallops having mean sizes of 75 to 80 mm.

As mentioned above, the scallops from the ex-

TABLE 4.—Lengths (millimeters) of calico scallops collected monthly from the experimental bed north of the main bed and commercial catch, 1972.

	Experimental bed			Commercial catch		
Month	Average length	Size range	Sample size	Average length	Size range	Sample size
Feb.	35.5	28-44	100	47.3	40-54	545
Mar.	37.4	30-47	150	46.3	37-55	510
Apr.	—	—	—	47.3	35-56	617
May	49.8	43-55	86	47.8	41-62	276
June	44.8	33-54	152	50.7	39-70	1,100
July	—	—	—	47.6	35-61	450
Aug.	45.0	39-57	127	50.8	36-59	400
Sept.	53.3	44-64	150	54.2	48-65	316
Oct.	50.5	42-57	100	55.0	43-65	101
Average length increase	17.8			8.7		

perimental area were consistently smaller than those from the commercial area (Table 4). Median sediment size and texture analyses data from the two areas were virtually identical (Table 3). There was some indication that organic values in the experimental area may be slightly higher than those from the commercial area (Table 3). Carriker (1959) noted that growth of *Mercenaria mercenaria* was faster in his low organic areas than in areas with higher organic percentages. This was the opposite of our findings.

Apparently the growth of the calico scallop is not related to chlorophyll a content for we noted primarily little difference between chlorophyll a content, regardless of sampling area (Figure 5).

FISHES OF THE CALICO SCALLOP BED

Some 4,461 fishes belonging to 49 families and 111 species were collected during the 51 cruises between 9 January and 23 October 1972. One additional species, *Scorpaena isthmensis,* was added to the faunal list during exploratory trips in 1971 and 1973. Pelagic, demersal, and benthic families and species were represented in the catches (Table 5). Of the total fishes landed (4,392) as part of the 1972 scallop catches, 985 were tagged and released to note movements, 1,655 were analyzed for food content, and 1,752 specimens were merely observed and identified. Most of the 112 species encountered were sporadic components of the scallop bed either as they passed north-to-south or east-to-west, depending on the season of the year.

Of the 112 species of fishes associated with the calico scallop bed, 94 or 84.0% can be considered Caribbean in their main distribution and abundance, while 7 (6.2%) were Virginian forms that had moved seasonally south of the Cape Hatteras barrier. Eleven species (9.8%) were those whose distribution ranges extended naturally over a broad north-south geographic area and could not be considered northern or southern faunal components. Controversy still exists whether that portion of the shelf off North Carolina is simply a part of an overall north-south temperate Virginia Province faunal region (Forbes 1856) or an area divided into a nearshore Virginia and offshore Gulf Stream influenced Carolinian Province (Gray and Cerame-Vivas 1963; Wells et al. 1964; Cerame-Vivas and Gray 1966; Gray et al. 1968; Bumpus 1973; Briggs 1974). Struhsaker (1969) and Schwartz (in press) have shown this area to be rich in fishes with an overall 70:30 ratio of southern to northern fishes, a condition far richer than that of the northern Gulf of Mexico, contrary to the findings of Briggs (1974).

Some 33 species dominated the 1972 catches, of which 21 species accounted for 77.1% of the fishes handled: *Stenotomus aculeatus* (413 specimens), *Synodus foetens* (386), *Paralichthys dentatus* (303), *Diplectrum formosum* (254), *Raja eglanteria* (252), *Orthopristes chrysopterus* (249), *Prionotus scitulus* (196), *Monacanthus hispidus* (174), *Centropristes striata* (122), *Balistes capriscus* (120), *Prionotus evolans* (116), *Hemipteronotus novacula* (104), *Leiostomus xanthurus* (104), *Mustelus canis* (95), *Lagodon rhomboides* (91), *Aluterus schoepfi* (85), *Paralichthys albigutta* (77), *Etrumeus teres* (75), *Urophycis regius* (74), *Syacium papillosum* (73), and *Ancylopsetta quadrocellata* (71).

A few species, notably *Raja eglanteria, Centropristes striata, Ancylopsetta quadrocellata,* and *Paralichthys dentatus,* seemed to occupy the beds throughout the year (Table 5). The loss of such species as *Prionotus evolans, Orthopristes chrysopterus,* and *Aluterus schoepfi* from the beds was evident as they moved shoreward during the summer months. *Mustelus canis* and *Urophycis regius* were winter components of the fauna prior to their movement northward or seaward away from the encroaching higher summer water temperatures. Others, such as *Diplectrum formosum, Mullus auratus,* and *Aluterus scriptus* occurred during or appeared late in the summer, apparently transported by meanders of the Gulf Stream (Webster 1961; Roe et al. 1971) from the south when water conditions met their usual tropical temperature requirements for existence. *Rhinoptera bonasus* was a good sample of a north-south transient in April and August as the schools moved past the area to other grounds (Schwartz 1965). *Halieutichthys* was an example of an offshore species apparently moving into shallower water with occasional incursions (Blanton 1971) of deep ocean water onto the shelf. As expected, bottom fishes of the families Bothidae, Soleidae, Triglidae, and hard shell crushers of the Balistidae and Tetraodontidae predominated (Table 5). The most exciting captures were *Letharchus velifer, Seraniculus pumilio, Prionotus ophryas,* and *Scorpaena isthmensis,* as their capture represented sizeable northward range extensions. McEachran and Eschmeyer (1973) have also recently noted the northward extension of *S. isthmensis.*

Nineteen species were tagged for movement

TABLE 5.—A list of fish species encountered during the various calico
T = tagged; F = food analysis; A= additional

Species	1971	Jan.-Feb.			March			April			May			June		
		T	F	A	T	F	A	T	F	A	T	F	A	T	F	A
Carcharhinus obscurus		—	—	—	—	—	—	1	—	—	—	—	—	—	1	—
Mustelus canis		6	3	20	21	7	—	14	23	1	—	—	—	—	—	—
Rhizoprinodon terraenovae		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Squalus acanthias		—	—	2	—	—	—	—	—	—	—	—	—	—	—	—
Squatina dumerili		—	—	—	—	—	—	1	1	—	—	—	—	—	—	—
Rhinobatos lentiginosus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Narcine brasiliensis		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Raja eglanteria		—	1	11	30	114	12	9	8	2	14	—	—	12	1	—
Dasyatis americana		—	—	—	—	—	—	5	1	1	—	—	—	1	—	—
D. centroura		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gymnura micrura		—	—	—	1	—	—	2	1	—	—	—	—	—	—	—
Myliobatis freminvillei		—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Rhinoptera bonasus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Manta birostris		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gymnothorax nigromarginatus saxicola		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Conger oceanicus		—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Letharchus velifer		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ophichthus ocellatus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Etrumeus teres		—	—	—	—	—	60	—	—	—	—	—	15	—	—	—
Anchoa hepsetus		—	—	—	—	—	—	—	—	57	—	—	—	—	—	—
Synodus foetens		—	1	13	6	75	70	—	—	16	9	47	10	—	2	—
S. poeyi		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Trachinocephalus myops	4	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Opsanus tau		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Porichthys porosissimus		—	—	—	—	3	—	—	—	—	—	1	—	—	—	—
Gobiesox strumosus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lophius americanus		—	—	—	—	2	—	—	1	—	—	—	—	—	—	—
Antennarius ocellatus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. scaber	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Halieutichthys aculeatus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ogcocephalus sp.		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Urophycis earli		—	—	—	—	—	—	—	—	3	—	—	—	—	—	—
U. regius	1	—	1	2	—	—	54	2	3	12	—	—	—	—	—	—
Rissola marginata		—	—	—	—	—	—	—	—	10	—	—	—	—	—	—
Fistularia tabacaria	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hippocampus erectus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Syngnathus springeri	3	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—
Centropristes ocyurus		—	—	15	—	—	—	—	—	—	1	2	—	5	—	—
C. philadelphicus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C. striatus	11	—	2	2	—	—	—	10	7	2	14	5	—	11	6	—
Diplectrum formosum	3	—	—	—	—	—	—	—	—	—	3	1	—	11	52	—
Serranus phoebe		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
S. subligarius		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Serraniculus pumilio		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rypticus maculatus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pristigenys alta	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pomatomus saltatrix		—	1	1	—	—	—	—	—	—	—	—	—	—	—	—
Caranx fusus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Decapterus punctatus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lutjanus vivanus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Haemulon aurolineatus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
H. plumieri		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Orthopristis chrysopterus		—	7	23	1	5	2	4	11	151	16	21	—	2	1	—
Archosargus probatocephalus		—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
Calamus bajonado		—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
C. leucosteus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lagodon rhomboides		—	10	75	—	—	—	—	—	5	—	—	—	—	—	—
Sparisoma radians		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Stenotomus aculeatus		—	5	13	3	20	16	11	12	171	10	45	—	4	1	—
Cynoscion nebulosus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C. regalis		—	—	6	—	—	—	—	—	—	—	—	—	—	—	—
Parequetus sp.	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Larimus fasciatus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Leiostomus xanthurus		—	3	10	—	—	—	—	1	—	—	1	—	—	—	—
Menticirrhus americanus		—	2	3	2	—	—	—	—	—	—	—	—	—	—	—
M. saxatilis		—	2	6	4	1	7	5	7	1	—	—	—	—	—	—
Micropogon undulatus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mullus auratus	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chaetodipterus faber		—	—	—	1	—	—	—	—	—	3	1	—	—	—	—
Chromis enchrysurus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Halichoeres bivittatus	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
H. caudalis	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hemipteronotus novacula	17	—	—	—	—	3	3	1	1	—	—	4	5	6	11	—
Astroscopus y-graecum		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Trichurus lepturus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Euthynnus alletteratus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

scallop cruises aboard commercial, research, and chartered vessels.
species encountered but not examined or tagged.

Species	July			August			September			October			1972 total			Total 1972
	T	F	A	T	F	A	T	F	A	T	F	A	T	F	A	
Carcharhinus obscurus	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	2
Mustelus canis	—	—	—	—	—	—	—	—	—	—	—	—	41	33	21	95
Rhizoprinodon terraenovae	1	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1
Squalus acanthias	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2
Squatina dumerili	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	2
Rhinobatos lentiginosus	—	—	1	—	—	1	—	—	1	—	—	—	—	—	3	3
Narcine brasiliensis	—	—	1	1	—	1	—	—	—	—	—	—	1	—	2	3
Raja eglanteria	8	1	—	18	6	—	1	2	—	—	2	—	92	135	25	252
Dasyatis americana	—	—	—	—	—	—	—	—	—	—	—	—	6	1	1	8
D. centroura	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	1
Gymnura micrura	—	—	—	—	—	—	—	—	—	—	—	—	3	1	—	4
Myliobatis freminvillei	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Rhinoptera bonasus	1	—	1	4	—	—	—	—	—	—	—	3	5	—	4	9
Manta birostris	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	1
Gymnothorax nigromarginatus saxicola	—	—	—	—	—	—	—	1	1	—	—	—	—	1	1	2
Conger oceanicus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Letharchus velifer	—	—	—	—	—	1	—	—	1	—	—	—	—	—	2	2
Ophichthus ocellatus	—	—	—	—	—	—	—	—	1	—	—	1	—	—	2	2
Etrumeus teres	—	—	—	—	—	—	—	—	—	—	—	—	—	—	75	75
Anchoa hepsetus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	57	57
Synodus foetens	—	4	—	—	54	32	—	12	5	—	5	25	15	200	171	386
S. poeyi	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	1
Trachinocephalus myops	—	2	—	—	5	1	—	—	—	—	—	—	—	8	1	9
Opsanus tau	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—	1
Porichthys porosissimus	—	2	—	—	2	1	—	—	—	—	—	1	—	8	2	10
Gobiesox strumosus	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	1
Lophius americanus	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	3
Antennarius ocellatus	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1
A. scaber	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Halieutichthys aculeatus	—	—	—	—	—	3	—	—	2	—	—	—	—	—	5	5
Ogcocephalus sp.	—	—	—	—	—	5	—	—	—	—	—	1	—	—	6	6
Urophycis earli	—	—	—	—	—	1	—	—	—	—	—	—	—	—	4	4
U. regius	—	—	—	—	—	—	—	—	—	—	—	—	2	4	68	74
Rissola marginata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	10
Fistularia tabacaria	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hippocampus erectus	—	—	—	—	—	2	—	—	1	—	—	—	—	—	3	3
Syngnathus springeri	—	—	1	—	—	1	—	—	1	—	—	—	—	—	5	5
Centropristes ocyurus	—	5	—	1	—	5	—	—	—	—	—	3	7	7	23	37
C. philadelphicus	—	—	3	—	—	3	—	—	4	—	—	1	—	—	11	11
C. striatus	2	4	—	12	7	1	6	19	—	2	7	3	57	57	8	122
Diplectrum formosum	2	11	4	—	3	27	—	—	73	—	—	67	16	67	171	254
Serranus phoebe	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	1
S. subligarius	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	1
Serraniculus pumilio	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	1
Rypticus maculatus	—	—	2	—	—	—	—	—	—	—	—	—	—	—	2	2
Pristigenys alta	—	—	—	—	—	2	—	—	1	—	—	4	—	—	7	7
Pomatomus saltatrix	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	2
Caranx fusus	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	1
Decapterus punctatus	—	—	—	—	—	2	—	—	—	—	—	—	—	—	2	2
Lutjanus vivanus	—	—	—	—	—	—	—	—	1	—	—	2	—	—	3	3
Haemulon aurolineatus	—	—	—	—	—	2	—	—	3	—	—	1	—	—	6	6
H. plumieri	—	—	—	—	1	3	2	—	1	—	—	—	2	1	4	7
Orthopristis chrysopterus	—	—	—	—	—	—	1	—	—	2	2	—	26	47	176	249
Archosargus probatocephalus	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1
Calamus bajonado	—	—	—	1	—	—	—	—	—	—	—	—	1	—	1	2
C. leucosteus	—	—	—	2	4	1	2	11	—	—	—	—	4	15	1	20
Lagodon rhomboides	—	—	—	—	—	1	—	—	—	—	—	—	—	10	81	91
Sparisoma radians	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1
Stenotomus aculeatus	1	5	—	6	2	3	—	3	2	42	8	30	77	101	235	413
Cynoscion nebulosus	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1
C. regalis	—	—	—	—	—	—	—	—	—	—	—	2	—	—	8	8
Parequetus sp.	—	—	—	—	—	—	—	—	2	—	—	—	—	—	2	2
Larimus fasciatus	—	—	—	—	—	—	—	—	—	—	—	4	—	—	4	4
Leiostomus xanthurus	—	—	—	—	—	—	—	85	—	1	—	—	1	90	10	101
Menticirrhus americanus	—	—	—	—	—	—	—	—	—	—	—	—	2	2	3	7
M. saxatilis	—	—	—	—	—	—	—	—	—	—	—	3	9	10	17	36
Micropogon undulatus	—	—	—	—	—	—	—	—	8	—	—	—	—	—	8	8
Mullus auratus	—	—	—	—	—	1	—	—	1	—	—	1	—	—	3	3
Chaetodipterus faber	—	1	—	4	—	—	—	—	—	2	2	9	10	4	8	23
Chromis enchrysurus	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	1
Halichoeres bivittatus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
H. caudalis	—	—	—	—	—	—	—	—	3	—	—	1	—	—	4	4
Hemipteronotus novacula	2	11	—	—	10	42	—	—	1	—	—	4	9	40	55	104
Astroscopus y-graecum	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	1
Trichurus lepturus	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1
Euthynnus alletteratus	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	1

Table 5.—Continued.

Species	1971	Jan.-Feb			March			April			May			June		
		T	F	A	T	F	A	T	F	A	T	F	A	T	F	A
Peprilus alepidotus		—	3	—	—	—	—	—	—	—	—	—	—	—	—	—
P. triacanthus		3	20	—	—	—	—	—	5	3	—	—	—	—	—	—
Scorpaena brasiliensis	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
S. calcarata	6	6	—	—	1	14	4	2	1	1	—	1	—	—	1	1
Bellator militaris	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Prionotus evolans		—	2	3	8	29	2	1	1	8	—	3	2	—	6	—
P. ophryas		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
P. roseus	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
P. scitulus		—	7	1	3	19	9	—	6	8	—	76	15	2	—	—
P. salmonicolor		—	—	1	—	1	1	—	—	7	—	—	25	—	—	—
P. tribulus		—	—	3	—	—	—	—	—	—	—	—	—	—	—	—
Ancylopsetta quadrocellata		—	—	5	—	10	2	4	1	—	6	1	—	14	1	—
Bothus sp.		—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Citharichthys macrops		—	—	2	—	2	—	—	—	6	—	—	3	6	—	—
Cyclopsetta fimbriata	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Etropus microstomus		—	—	—	—	1	1	—	—	—	—	—	—	—	—	—
E. rimosus		—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Paralichthys albigutta		—	11	—	8	11	9	9	—	1	1	—	—	—	—	—
P. dentatus		—	21	—	20	39	32	48	6	—	22	—	2	36	2	—
P. lethostigma		—	—	9	28	4	4	—	—	1	—	—	—	—	—	—
P. squamilentus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Scophthalmus aquosus		—	—	2	—	—	—	—	—	—	—	—	—	—	—	—
Syacium papillosum	3	3	—	—	—	7	1	—	3	—	4	—	1	10	—	—
Gymnachirus melas	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Trinectes maculatus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Alutera schoepfi		—	—	—	3	8	—	—	—	—	—	—	—	—	—	—
A. scriptus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Balistes capriscus	1	1	—	—	1	3	1	4	—	—	6	4	—	30	36	—
Monacanthus hispidus		—	—	1	2	7	—	1	—	—	5	—	1	28	7	—
Lactophrys quadricornis		—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Sphoeroides dorsalis		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
S. maculatus		—	18	50	6	145	19	—	5	7	—	1	2	—	—	—
S. spengleri		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chilomycterus antillarum		—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
C. schoepfi		—	—	—	—	4	1	1	—	—	—	1	—	—	—	—
Subtotal		20	120	281	149	534	312	135	105	478	115	215	81	178	129	2
Total	69		421			995			718			411			309	

studies. Of those tagged, *Paralichthys dentatus* (184 specimens), *Monacanthus hispidus* (107), *Raja eglanteria* (92), *Stenotomus aculeatus* (77), *Balistes capriscus* (66), *Centropristes striata* (57), *Mustelus canis* (41), *Ancylopsetta quadrocellata* (40), *Aluterus scriptus* (35), and *Paralichthys lethostigma* (35) accounted for 74.3%. Of the 985 fishes tagged, 17 (1.7%) were recaptured involving 11 species: *Centropristes striata, Balistes capriscus, Aluterus schoepfi, Centropristes ocyurus, Calamus bajonado, Monacanthus hispidus, Paralichthys albigutta, P. dentatus, Rhinoptera bonasus, Raja eglanteria,* and *Stenotomus aculeatus. Paralichthys dentatus* and *Balistes capriscus* accounted for 6 and 2 of the recaptures respectively, while all others were single recaptures. Most recaptures were returned from near their release point on the bed. The longest period at liberty was 8 days. This, in the light of the intense fishing of the 13 boats that composed the 1972 fleet and the few recaptures, suggested that the fish population over the scallop bed was large, constantly moving, and subject to constant recruitment from elsewhere.

Stomach analysis of 1,655 of the 33 most frequently encountered fishes (Table 6) revealed that the stomachs of most of the fishes over the bed usually contained food even though all samples were made only during daylight hours; 89.4% had scallops or other food as part of the stomach contents. *Sphoeroides maculatus, Stenotomus aculeatus, Diplectrum formosum, Orthopristes chrysopterus, Monacanthus hispidus, Balistes capriscus, Centropristes striata, Mustelus canis,* and *Synodus foetens* (in descending order of species whose stomachs contained scallops) were found to be scallop predators (Table 6). Small as well as large individuals of these species had parts or whole scallops in their stomachs and digestive tracts (Table 6). These species fed either by cracking the scallop shell with their beaklike jaws (*Balistes, Sphoeroides*) or by finding dying or cracked (possibly a result of the fishing activity) individuals (*Stenotomus, Diplectrum, Orthopristes*). It was surprising that bottom feeders of the families Bothidae (*Paralichthys albigutta, P. lethostigma*), Soleidae (*Trinectes maculatus*), Rajidae (*Raja eglanteria*), Labridae (*Hemip-*

Species	July			August			September			October			1972 total			Total 1972
	T	F	A	T	F	A	T	F	A	T	F	A	T	F	A	
Peprilus alepidotus	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	3
P. triacanthus	—	—	—	—	—	—	—	—	—	—	—	—	3	25	3	31
Scorpaena brasiliensis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
S. calcarata	1	3	—	—	3	—	—	1	1	—	—	1	10	24	8	42
Bellator militaris	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Prionotus evolans	3	7	—	3	12	5	—	7	1	1	8	4	16	75	25	116
P. ophryas	—	—	—	—	—	1	—	—	3	—	—	—	—	—	4	4
P. roseus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
P. scitulus	—	16	—	—	19	1	—	2	5	—	—	7	5	145	46	196
P. salmonicolor	—	—	—	—	—	8	—	—	3	—	—	—	—	1	45	46
P. tribulus	—	—	—	—	—	—	—	—	1	—	—	—	—	—	4	4
Ancylopsetta quadrocellata	9	2	—	6	3	1	1	1	4	—	—	—	40	19	12	71
Bothus sp.	—	—	—	—	—	1	—	—	1	—	—	1	—	—	4	4
Citharichthys macrops	—	—	—	—	1	10	—	—	4	—	—	—	6	3	25	34
Cyclopsetta fimbriata	—	—	—	—	—	—	—	—	1	—	—	1	1	—	2	3
Etropus microstomus	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	2
E. rimosus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Paralichthys albigutta	—	—	—	10	3	1	3	—	5	2	—	3	33	25	19	77
P. dentatus	24	4	—	17	1	—	11	2	1	6	6	3	184	81	38	303
P. lethostigma	—	—	—	1	—	—	5	—	—	1	—	3	35	4	17	56
P. squamilentus	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1
Scophthalmus aquosus	1	—	—	—	—	—	—	—	—	—	—	—	1	—	2	3
Syacium papillosum	1	1	—	1	4	33	—	—	3	—	—	1	19	15	39	73
Gymnachirus melas	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1	1
Trinectes maculatus	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1
Alutera schoepfi	3	—	—	12	26	2	6	14	—	3	8	—	27	56	2	85
A. scriptus	35	11	—	—	1	1	—	—	—	—	—	—	35	12	1	48
Balistes capriscus	8	4	—	10	5	—	6	1	—	—	—	—	66	53	1	120
Monacanthus hispidus	34	13	—	28	32	5	7	—	1	2	—	—	107	59	8	174
Lactophrys quadricornis	—	—	1	—	—	—	—	—	—	—	—	—	—	—	2	2
Sphoeroides dorsalis	—	—	2	—	—	1	—	—	—	—	—	2	—	—	5	5
S. maculatus	—	1	—	—	18	1	—	6	8	—	4	—	6	198	87	291
S. spengleri	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	1
Chilomycterus antillarum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
C. schoepfi	—	—	—	—	1	—	—	1	—	—	—	3	1	7	4	12
Subtotal	136	108	17	137	223	219	51	169	161	64	52	201	985	1,655	1,752	
Total		261			579			381			317			4,392		4,392
														Grand total		4,461

teronotus novacula), and other Balistidae (*Aluterus schoepfi*) were not active scallop predators.

Our observations agree with Roe et al. (1971), who noted that *Sphoeroides* is an active predator of calico scallops. While *Dasyatis centroura* is a possible predator (Struhsaker 1969) neither it, the dasyatids *D. americana* and *Gymnura micrura*, nor the myliobatid, *Rhinoptera bonasus*, fed on scallops.

MACROINVERTEBRATE ASSOCIATES AND PREDATORS

Field observations yielded 60 species of macromolluscs, 25 crustaceans, 12 echinoderms, 4 coelenterates, and 1 annelid as associates of the bed (Table 7). These species, their numbers, and abundances varied by season throughout the bed. Species found in 50 or more percent of the samples which may be considered the macroinvertebrates common to the beds were: *Eucrassatella speciosa, Arcinella cornuta, Cassis madagascariensis, Pleuroploca gigantea, Octopus vulgaris, Loligo pealei, Calappa falmmea, Hepatus epheliticus, Astropecten articulatus, Luidia alternata, L. clathrata, Hemipholis elongata, Toxopneustes variegatus*, and *Encope emarginata*.

Luidia clathrata and *Astropecten articulatus* occurred abundantly throughout the bed during all seasons and were predators of scallops (Table 7). The following were found less abundantly and were suspected predators of calico scallops: *Asterias forbesii, Busycon carica, B. contrarium, B. spiratum, Fasciolaria hunteria, F. tulipa, Loligo pealei, Murex fulvescens, M. pomum, Octopus vulgaris, Pleuroploca gigantea, Polinices duplicatus, Strombus alatus, Arenaeus cribrarius, Calappa flammea, Hepatus epheliticus, Libinia emarginata, Ovalipes quadulpensis*, and *Portunus spinimanus*.

The most common sea stars on the 1972 calico scallop grounds were *Astropecten articulatus, Luidia alternata*, and *L. clathrata*. *Goniaster americanus, Echinaster brasiliensis, Asterias forbesi*, and *Gorgonocephalus arcticus* were noted in lesser numbers (Table 7). Identifications were

TABLE 6.—Analysis of 1,655 stomach contents from 46 species of fishes captured on the scallop grounds during commercial operations between February and October 1972.

Species	Cruises occurred in	Specimens examined	Size range	Number eating		
				Scallops	Other food	Empty
Carcharhinus obscurus	2	1	960		1	
Mustelus canis	8	33	440-972	13	15	5
Squatina dumerili	2	1	1,160		1	
Raja eglanteria	20	135	136-580	7	127	1
Dasyatis americana	4	1	676		1	
Gymnura micrura	4	1	415		1	
Gymnothorax nigromarginatus saxicola	2	1	276		1	
Synodus foetens	23	200	98-426	11	163	26
Trachinocephalus myops	6	8	170-216	1	2	5
Opsanus tau	2	1	246		1	
Porichthys porosissimus	6	8	146-210		8	
Lophius americanus	4	3	560-716	1	1	1
Urophycis regius	2	4	110-208	1	1	2
Centropristis ocyurus	4	7	112-172	6	1	
C. striata	15	57	92-325	21	28	8
Diplectrum formosum	9	67	46-282	37	23	7
Pomatomus saltatrix	3	1	138		1	
Haemulon plumieri	6	1	230		1	
Orthopristis chrysopterus	14	47	116-216	36	6	5
Calamus senta	6	15	120-225		15	
Lagodon rhomboides	4	10	87-122		10	
Stenotomus aculeatus	22	101	90-256	64	27	10
Leiostomus xanthurus	4	90	144-188	1	86	3
Menticirrhus americanus	2	2	170-262		2	
M. saxatilis	5	10	190-280	1	8	1
Chaetodipterus faber	9	4	286-290		4	
Hemipteronotus novacula	17	40	128-172	7	26	7
Peprilus alepidotus	2	3	118-156		3	
P. triacanthus	2	25	97-156	1	4	20
Scorpaena calcarata	15	24	64-142	1	23	
Prionotus evolans	19	75	196-342	2	61	12
P. salmonicolor	6	1	186-222		1	
P. scitulus	19	145	134-268	2	136	7
Ancylopsetta quadrocellata	28	19	170-290		19	
Citharichthys macrops	11	3	120-142		3	
Etropus microstomus	3	1	158		1	
Paralichthys albigutta	21	25	200-289		25	
P. dentatus	42	81	153-370		81	
P. lethostigma	14	4	210-500		4	
Syacium papillosum	8	15	86-300	1	13	1
Aluterus schoepfi	14	56	342-390		56	
A. scriptus	3	12	90-222	1	5	6
Balistes capriscus	18	53	105-356	20	28	5
Monacanthus hispidus	14	59	92-222	23	20	16
Sphoeroides maculatus	21	198	68-268	77	94	26
Chilomycterus schoepfi	6	7	72-142	2	4	1
Total, number				337	1,143	175
percent				20.4	69.0	10.6

based upon Gray et al. (1968) and Downey (pers. commun.).

Roe et al. (1971) suggested that *Asterias forbesi* may be a major predator on the calico scallops of the Cape Canaveral grounds. The low total percent of its occurrence on the 1972 North Carolina calico scallop grounds (Table 7) precludes this assumption for the 1972 fishery. Stomachs of *A. forbesi* were not examined because it everts its stomach when feeding (Hyman 1955:369). Hyman (1955) made no mention of the feeding habits of sea stars belonging to the Goniasteridae, Echinasteridae, or the Gorgonocephalidae. Stomachs of species belonging to these families (*Goniaster americanus, Echinaster brasiliensis,* and *Gorgonocephalus arcticus*) contained no recognizable material. What they were feeding upon is not known but, in light of their small numbers on the scallop beds and the lack of scallops in their stomachs, it is assumed that they were not significant scallop predators on the 1972 bed.

Luidia alternata frequented the calico scallop bed yet was not as common as either *L. clathrata* or *Astropecten articulatus* (Table 7). Stomach contents yielded no calico scallops. Several specimens were found in the field feeding upon smaller *A. articulatus*. One large living specimen, held in an experimental tank under controlled environmental conditions with living calico scallops, showed no interest in the scallops but was seen feeding upon *A. articulatus* and *L. clathrata*. It did attempt unsuccessfully to feed on a *Asterias forbesi*

TABLE 7.—Macroinvertebrate fauna of offshore calico scallop beds in 1972 by season and areas of good and poor catches. N = number of samples, data listed as percent of N.

Taxa	Mar.-Apr. N = 14	May-June N = 10	July-Aug. N = 14	Sept.-Oct. N = 10	Total N = 48	Good scallop catches N = 40	Poor scallop catches N = 8
COELENTERA							
Renillidae:							
Renilla reniformis	7				2	2	
Actiniaria (sea anemones)	14	20			8	10	
Madreporaria (corals)				20	4	5	
ANNELIDA							
Aphroditidae:							
Aphrodita hastata	7				2	2	
MOLLUSCA							
Arcidae:							
Arca imbricata			7		2	2	
A. zebra	14	10	7	10	10	12	
Anadara floridana	36	20	21		21	25	
Noetia ponderosa			14		4	5	
Mytilidae:							
Brachidontes modiolus	14	30	36		21	25	
Pteriidae:							
Pteria colymbus	14			10	6	15	
Pectinidae:							
Aequipecten muscosus				10	2	2	
Argopecten gibbus	93	100	71	80	85	100	13
Lyropecten nodosus		10	21	10	10	10	13
Pecten raveneli	21	30	21	30	25	28	13
Ostreidae:							
Ostrea permollis			7	20	6	7	
Chamidae:							
Arcinella cornuta	43	40	79	30	50	55	25
Chama macerophylla		10			2	2	
Crassatellidae:							
Eucrassatella speciosa	43	40	86	10	48	50	38
Cardiidae:							
Dinocardium robustum	7	10	14	20	13	13	13
Laevicardium multilineatum	21	10	21	10	17	15	25
Veneridae:							
Chione intapurpurea	7	10	43	30	23	18	50
C. latilirata	29	20	64	40	40	35	63
Macrocallista maculata	57	20	43	20	38	43	13
M. nimbosa		10			2	2	
Solenidae:							
Ensis directus				10	2	2	
Tellinidae:							
Tellina magna			7		2		13
T. nitens				10	2	2	
Solecurtidae:							
Solecurtus cumingianus	7				2	2	
Trochidae:							
Calliostoma euglyptum			7	10	4		25
Turbinidae:							
Astraea phoebia			7		2		13
Turbo castanea		10	14	30	13	15	13
Architectonicidae:							
Architectonica nobilis		10		10	4	5	
Cerithiidae:							
Cerithium litteratum							
Xenophoridae:							
Xenophora conchyliophora	14	30	7	20	17	20	
Strombidae:							
Strombus alatus	14	50	57	30	38	45	
S. costatus			7		4	2	
Cypraeidae:							
Cypraea cervus			14		4	5	
Naticidae:							
Natica canrena			7	10	4	5	
Polinices duplicatus	36	20	50	20	33	35	25
P. duplicatus eggs	7				2	2	
Sinum maculatum	7	10	7	20	10	12	
Cassididae:							
Cassis madagascariensis	21	80	79	50	56	60	38
C. madagascariensis eggs		20			4	5	
Cypraecassis testiculus			7		2	2	
Phalium granulatum	21	20	36	20	25	25	25
P. granulatum eggs		10			2	2	
Cymatidae:							
Distorsio clathrata	7	20	21		13	15	
Tonnidae:							
Oocorys abyssorum							
Tonna galea	7	40	7		13	15	

Table 7.—Continued.

Taxa	Mar.-Apr. $N = 14$	May-June $N = 10$	July-Aug. $N = 14$	Sept.-Oct. $N = 10$	Total $N = 48$	Good scallop catches $N = 40$	Poor scallop catches $N = 8$
Ficidae:							
Ficus communis	7	20	14		10	12	
Muricidae:							
Eupleura caudata			7		2	2	
Murex dilectus			7		2		13
M. fulvescens	29	30	71		35	40	13
M. fulvescens eggs			14		4	5	
Murex pomum	21	30	29	40	29	28	38
Thais haemastoma floridana				10	2	2	
Melongenidae:							
Busycon canaliculatum			7		2	2	
B. carica		20	7	20	10	10	13
B. contrarium	29	10		20	15	15	13
B. contrarium eggs	21				6	7	
B. spiratum	21	20	14	30	21	23	13
B. spiratum eggs	14				4	5	
Fasciolariidae:							
Fasciolaria lilium hunteria	7	40	57	20	31	30	38
F. l. hunteria eggs			14		4	5	
F. tulipa	21	30	21	10	21	23	13
F. tulipa eggs	7				27	2	
Pleuroploca gigantea	43	70	50	70	56	55	63
P. gigantea eggs		10	7	4	5		
Olividae:							
Oliva sayana Ravenel	43	10	50	20	33	35	25
Cancellariidae:							
Cancellaria reticulata	7						
Conidae:							
Conus delessertii	7	30	14		13	15	
Octopodidae:							
Octopus vulgaris	71	70	93	60	75	75	75
Loliginidae:							
Lolliguncula brevis	7				2	2	
Loligo pealeii	71	50	93	60	71	70	75
ARTHROPODA							
Stomatopoda:							
Gonodactylus aerstedi	21	20	14		15	17	
Penaeidae:							
Penaeus sp.	29	20	7	20	19	22	
Sicyonia brevirostris	21	10	29	30	23	21	13
Scyllaridae:							
Scyllarides nodifer	7	20		10	8	10	
Porcellaridae:							
Porcellana sayana	14				4	5	
Paguridae:							
Pagurus sp.	7			10	4	5	
P. annulipes		60	64	40	40	40	38
P. pollicaris		40	64	40	35	35	38
Raninidae:							
Ranilia muricata	14		7		6	7	
Calappidae:							
Calappa angusta	7			10	4	5	
C. flammea	64	60	79	60	67	73	38
Hepatus epheliticus	43	70	64	70	60	65	38
Osachila sp				10	2		13
Portunidae:							
Ovalipes quadulpensis	21				6	7	
O. ocellatus	21	30	36	10	25	25	25
Portunus gibbesii	57	40	36	30	42	45	25
P. spinimanus	7			30	8	10	
Callinectes sapidus							
Arenaeus cribrarius	7	10			4	5	
Cancridae:							
Cancer irroratus	7				2	2	
Majidae:							
Libinia emerginata	36	50	36	40	40	43	25
Stenocionops furcata coelata				10	2	2	
Parthenopidae:							
Parthenope serrata	14				4	5	
P. pourtelesii				10	2	2	
Xiphosura:							
Xiphosura polyphemus	43	50	50	10	40	40	38
ECHINODERMA							
Astropectinidae:							
Astropecten articulatus	100	90	93	80	92	93	88
Luidiidae:							
Luidia alternata	57	90	86	20	65	70	38
L. clathrata	100	100	93	90	96	98	88

Table 7.—Continued.

Taxa	Mar.-Apr $N = 14$	May-June $N = 10$	July-Aug $N = 14$	Sept.-Oct $N = 10$	Total $N = 48$	Good scallop catches $N = 40$	Poor scallop catches $N = 8$
Goniasteridae:							
Goniaster americanus	7	40	7		13	13	13
Echinasteridae:							
Echinaster brasiliensis	14	30	14	30	21	23	13
Asteriidae:							
Asterias forbesi	7	30			8	10	
Gorgonocephalidae:							
Gorgonocephalus arcticus		10		10	4	3	13
Amphiuridae:							
Hemipholis elongata	79	70	64	60	69	73	50
Arbaciidae:							
Arbacia punctulata	7	60	64	60	46	45	50
Toxopneustidae:							
Toxopneustes variegatus	36	80	79	60	63	65	50
Scutellidae:							
Encope emarginata	64	50	71	30	56	60	38
Cucumariidae:							
Thyone briareus	29			10	10	12	

and was noted to have killed a large *Strombus alatus*. Hyman (1955:369) pointed out that species of *Luidia* eat mainly other echinoderms. At this time, we do not consider *L. alternata* a calico scallop predator.

Luidia clathrata was a predator of calico scallops (Table 8). Between March and June we found small numbers of scallop valves (ranging from 0.9 to 11.6 and 21.1 to 45.3 mm) in *L. clathrata* stomachs (Table 9). Maximum predation took place (April) just as calico scallop spawning began. Why large scallops (21-45 mm lengths) were fed on only in March and April is not known. The data does indicate that numbers of *Luidia* (Table 10) large enough (110 to 160 mm?) to swallow the available scallops (28 to 70 mm length) were more available during March through June. Preliminary observations on *L. clathrata* kept in the laboratory indicated that they will feed readily on calico scallops, digestion occurring within 24 h. Hulings and Hemlay (1963) found *L. clathrata* to engulf sediments and utilize whatever was available as food.

Wells et al. (1961) suggested that *A. articulatus* was a nonselective feeder, while Porter (1972b)

TABLE 9.—Average number of calico scallop valves found per month in stomach samples of sea stars *Astropecten articulatus* and *Luidia clathrata* sampled in 1972 on the producing calico scallop beds off North Carolina.

Month	*Astropecten articulatus* No./100 stomachs[1]	*Astropecten articulatus* No. stomachs examined	*Luidia clathrata* No./100 stomachs[1]	*Luidia clathrata* No. stomachs examined
Feb.	1	85	0	71
Mar.	7	226	6	87
Apr	7	151	28	178
May	158	67	17	66
June	29	314	7	311
July	8	86	3	36
Aug	2	154	0	56
Sept.	7	89	0	43
Oct.	3	67	0	20

[1]Approximate number.

TABLE 10.—Monthly lengths (millimeters) for sea stars captured on the calico scallop beds in 1972.

Month	*Astropecten articulatus* Average arm length	*Astropecten articulatus* Size range	*Astropecten articulatus* Sample size	*Luidia clathrata* Average arm length	*Luidia clathrata* Size range	*Luidia clathrata* Sample size
Feb.	61.6	34-101	109	92.7	46-142	72
Mar.	63.3	24-111	433	95.6	58-155	134
Apr	60.0	18-124	176	91.2	27-166	227
May	58.9	35-122	125	88.2	40-140	110
June	61.1	25-134	497	88.8	50-160	315
July	64.8	28-103	112	89.6	61-122	42
Aug.	64.5	28-120	169	84.6	28-112	85
Sept.	83.1	35-136	113	87.0	51-134	44
Oct	62.2	23-124	101	89.6	23-124	22

TABLE 8.—Lengths (millimeters) of calico scallop valves removed from stomachs of sea stars *Astropecten articulatus* and *Luidia clathrata* collected on the calico scallop beds during the 1972 catch season.

Sea star	Feb.	Mar	Apr.	May	June	July	Aug.	Sept.	Oct.
Astropecten articulatus:									
Average valve length	1.8	2.4	1.9	2.3	3.0	2.9	2.3	2.9	4.5
Size range	1.8	1.6-3.8	0.7-4.3	0.9-3.6	0.7-6.4	2.3-3.6	1.4-2.6	1.7-2.6	3.3-5.6
Number valves found	1	8	10	62	39	5	4	5	2
Luidia clathrata:									
Average valve length	—	4.3	1.9	2.4	3.3	4.2	—	—	—
		33.9	43.7		21.1				
Size range	—	2.4-11.6	0.9-6.9	1.4-3.5	1.0-6.4	4.2-4.2	—	—	—
		30.0-40.4	41.0-45.3		21.1				
Number valves found	—	5	39	9	14	1	—	—	—
		8	6		1				

showed that large numbers of recently set calico scallops may be eaten by *A. articulatus* and that though continued examination of their stomach contents, knowledge may be gained concerning when and where calico scallop setting takes place. During May and June 1972, numerous small scallop valves appeared in the stomachs of this sea star (Table 10). Valve numbers/100 stomachs were not nearly as many as the 3,000/100 stomachs reported by Porter (1972a) for June 1971. It is inferred from this that the 1972 scallop set on the sampled grounds was relatively small. Note that numbers of dead scallop shells increased from July through October when the fishery collapsed (Table 11). Also, the presence of *L. clathrata* decreased while *A. articulatus* presence increased during the March to October period (Table 11).

Stomach content data (Table 10) suggested that if there were scallop spawnings following the initial May spawning as we have theorized, then the set from these and the May spawnings either did not survive after June or the setting occurred in an area not covered by the sampling. Stomach analysis data of sea stars continues to be worked up and evaluated.

TABLE 11.—Average monthly numbers of dead shells and sea stars per bushel catch (*N*) occurring on the calico scallop beds in 1972.

Month	*N*	Dead shells	*Luidia clathrata*	*Astropecten articulatus*
Mar	13	23	8	5
Apr.	8	19	5	4
May	2	19	1	2
June	8	22	1	2
July	7	106	2	6
Aug.	11	220	3	3
Sept.	4	134	1	8
Oct.	1	290	2	55

DISCUSSION

We had expected to find that the calico scallop bed(s) that sustained the 1972 North Carolina fishery to have been distinct in either physical, chemical, or biological features. Instead, few differences were found which could be pinpointed as factors that made the bed(s) more unique than the surrounding shelf areas. We noted that bottom texture within and without the beds studied were nearly identical (Table 3). Likewise, no extremes of water temperatures, salinities, or phytoplankton population (as measured by chlorophyll a levels) seemed to exist in 1972. While the fish and invertebrate faunas were diverse and speciose, they too were little different from that noted from the nearby reefs or areas (Pearse and Williams 1951; Wells et al. 1964; Cerame-Vivas and Gray 1966). Seasonal shifts in the fishes and invertebrates inhabiting the bed(s) occurred but these were directly related to seasonal water temperatures, salinities, or their natural migrating movements (Tables 5, 7). Most populations of fishes apparently moved over the bed(s) constantly, some 24 species (of 33 most abundant) feed on scallops. Of the macroinvertebrates, 3 species of sea stars and 19 other macroinvertebrates were predators. Whether the fishes and sea stars or other macroinvertebrate predators, which were definite predators of calico scallops, were attracted to the area because of the scallops or the activities of the fishery, which created available food in the form of broken scallops, remains unresolved. One interesting correlation was noted in that the painted wrasse, *Halichoeres caudalis*, appeared over the bed, in September and October, as increased numbers of dead scallops occurred just prior to the demise of the 1972 fishery on 28 October. This relationship has also been noted for the Cape Canaveral calico scallop beds of Florida (George Miller pers. commun.).

While we document the fish and macroinvertebrate faunas and the ecology of a North Carolina bed(s) that sustained the 1972 fishery, we are still at a loss as to what creates the vacillations of scallop availability in a bed or why one bed prevails over another during any one or succeeding years. Note that while the experimental bed was fished and did possess scallops throughout 1972, it as well as the commercial bed failed to support scallops in the years 1973 through 1976. We cannot ultimately conclude that the 1972 bed and fishery collapsed as a sole result of overfishing but that the levels of scallops available after 28 October could not economically support the fleet. Sampling the planktonic stages of calico scallops may resolve the repopulation aspects of the beds for we still do not know whether we are simply at the northern edge of its range, which may be dependent on larval drift and recruitment from more southern areas, or are dealing with a population dependent upon native larvae for repopulation. Additional field observations of the shelf water mass movements and how they affect the survival, growth, and existance of scallops needs refinement while laboratory experiments which vary a number of ecological parameters will hopefully

resolve what permits a calico scallop bed to exist.

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In galley: we anticipate Rick Dawson's revision of *Stenotomus* and list our *S. caprinus* as *S. aculeatus*.

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NOTES

ENERGY FOR MIGRATION IN ALBACORE, *THUNNUS ALALUNGA*

The relations between immigrants and residents of a specific fishing ground can likely be evaluated from examination of the relative fat content of individuals from a time sequenced sampling of the fishery. These kinds of information are not yet estimable for pelagic populations.

The problem of energy availability and utilization in migrations of fish is a perplexing one. Migrations are energetically quite expensive unless a fish is passively carried by currents. Recently recorded migrations of two tagged albacore, *Thunnus alalunga* (Bonnaterre), across the Pacific Ocean indicate that they traveled an average of 48 km/day (Japanese Fisheries Agency 1975). As these fish were approximately 80 cm long on release, the average migration speed was about 0.65 body lengths/s (55.6 cm/s). This is well within the range of observed swimming speeds for this species. These albacore were reported to have traveled from lat. 35°44′N, long. 171°37′E (Figure 1, point E) to lat. 47°00′N, long. 125°30′W (Figure 1, point F), a distance of 5,239 km in 110 days. The caloric equivalent, in grams of fat,[1] utilized by these two fish at the estimated rate of travel of about 55 cm/s would be about 1,450 g or 14.5% of their expected weight at the onset of migration. Although great amounts of feed would not be necessary for this migration given the 1 kcal/g average available caloric content for forage (Sharp and Francis 1976), the albacore has been reported to have up to 18.2% fat in the edible flesh portions (Sidwell et al. 1974). Muscle tissue constitutes 58.2% of the total body weight of albacore (Dotson unpubl. data) which means up to 10.6% body weight in fat has been observed, a value approaching that necessary to provide the caloric energy for these migrations.

There is little doubt that albacore do not migrate directly, that feeding does occur, and that the fish probably do grow in overall length and

[1]9.4 kcal/g fat.

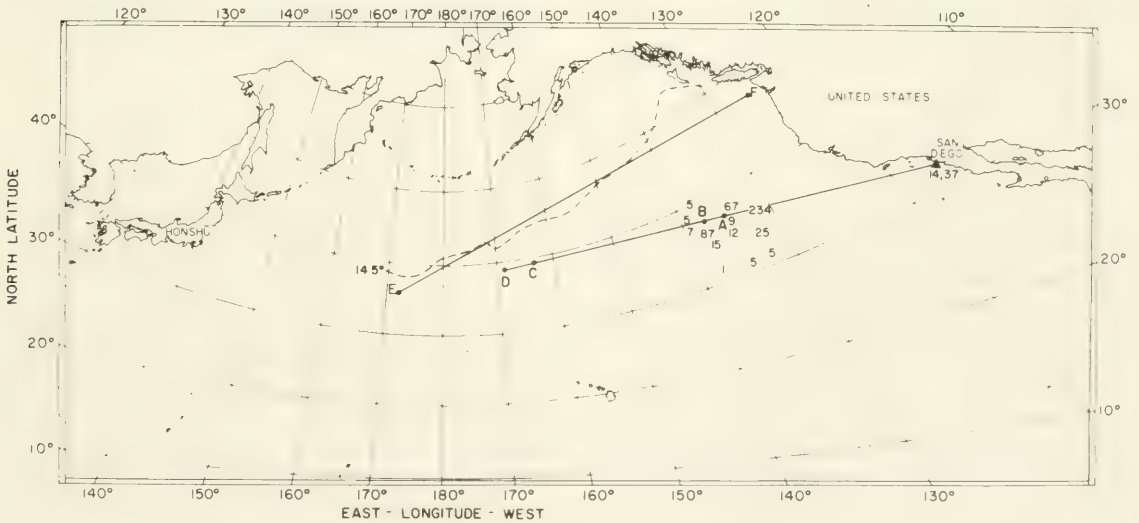

FIGURE 1.—A great circle plotting chart is shown and the quantity and location of albacore samples is indicated by the numerals. A length-mass equation was developed for the 477 albacore caught west of long. 130°W during June 1974. The numbers 14 and 37 near San Diego represent the samples collected in July and September 1975, respectively. Using ▲ as the origin the letters A and B along the line represent the distances which a 63-cm albacore could swim utilizing 404 g of fat at A, its minimum speed; B, the observed diurnal-nocturnal activity level. Points C and D on the same line represent the distance that the 65-cm fish with the greatest observed mass deficit (999 g) could have traveled utilizing the energy of this quantity of fat at the two respective activity levels described above. Points E and F are the release and recapture positions of two albacore tagged by Japanese researchers. The minimum temperature habitat limit of albacore (14.5°C) is depicted by a dashed line. The great circle route does not differ markedly from this boundary but likely represents a conservative estimate of the total distance traveled between points E and F.

mass during the migratory period. What appears to be an important question is whether or not the migrations of albacore and other tunas are extra demanding, meaning sufficient short-term energy is required to induce fat store utilization even though feeding is still accomplished. Too often the concepts of growth and fat deposition are integrated such that it is considered unlikely that morphological growth can take place during fat store utilization. Certainly from observations of adolescent growth in mammals it is obvious that there is no necessary dichotomy here. The two processes require separate biochemical pathways and are very likely separated temporally, well within the standard day.

In a preliminary effort to examine the question of fat utilization, the length-mass relationship of albacore collected offshore preceding their appearance in the onshore eastern Pacific surface fishery has been compared with fish freshly arrived in this fishery, and with fish which have presumably been grazing and reconditioning for the postsummer exodus from the onshore area. Calculations from these data support the hypothesis that fat stores are utilized for migration energy.

We hope that these calculations and subsequent inferences will stimulate further research into the considerable problem of highly variable length-mass information and its potential use in studies of migratory fishes.

Observations

In June 1974, 477 albacore 463 to 794 mm long were captured in the area between long. 130° to 140°W and lat. 30° to 40°N (Figure 1). A curve was fitted by regression to the length-mass data from these fish resulting in the equation (Dotson 1977),

$$M = 4.514 \times 10^{-5} L^{2.8746} \quad (1)$$

where M is the mass in grams and L the fork length in millimeters. Measured values fell within 250 g of the regression line.

Mass and length measurements were made on 14 albacore (600 to 657 mm FL, mean 631) collected during July and 37 fish (516 to 851 mm FL) collected during September 1975, in a region 110 km south of San Diego, Calif. (Figure 1). The mass of September-caught albacore was not different from those estimated by the length-mass regression curve. The mass of July-caught albacore, however, averaged 404 g below those estimated by regression (range: 172 g greater to 999 g less). Analysis of body densities indicated that the mass deficit of the albacore caught in July was probably due to fat loss, or simply stated, as a fish of a given length gets lighter its density increases (Dotson 1977).

The albacore fishery near the coast commenced in July 1975. The albacore in this fishery are known to migrate from the offshore region (Laurs and Lynn in press), and it is assumed, therefore, that the mass (fat) deficit was utilized as an energy source during migration to the coast.

Calculations and Inferences

Using the observed mass deficits observed in the July 1975 sample, it is possible to estimate the migration path length assuming 1) little or no growth occurs during the migration, and 2) the fat utilized is the only energy source during migration.

Based upon studies of swimming energetics of tunas, Sharp and Francis (1976) estimated the relation between swimming speed (V) in centimeters per second, fork length (l) in centimeters, and the swimming caloric expenditure per unit time (C_s) in kilocalories per hour. The basic equation for this relation, in calories utilized per hour, is as follows:

$$C_s = 8.7 \times 10^{-8} (l)^2 (V)^3 Cd. \quad (2)$$

The coefficient of drag (Cd) is estimated using the relation (Sharp and Francis 1976)

$$Cd = 0.262 \exp [-(4.805 \times 10^{-6}) Re] \quad (3)$$

where Re (Reynolds number) $= lV/\nu$ (at $Re \geq 6.8 \times 10^5$, $Cd = 0.01$), ν is the kinematic viscosity of seawater, approximated by the value 0.01.

Sharp and Francis (1976) also estimated the metabolic maintenance energy (C_m) (i.e. stasis energy requirements) for tunas to be 1 g cal/g per h. The metabolic weight (W_{met}) is approximated by the relation

$$W_{\text{met}} = (M_f)^{0.8} \quad (4)$$

$$C_m = W_{\text{met}} \times 10^{-3} \text{ kcal/g per h} \quad (5)$$

where M_f is the mass of the fish in grams.

Assuming that the mean mass deficit of 404 g of

the albacore caught in July was fat loss and given that fat yields about 9.4 kcal/g, less ~15% due to the cost of fat mobilization (SDA), leaving about 8.0 kcal/g, the caloric value of the fat loss is 3,272 kcal. The mean length of the albacore in the July sample was 63 cm with a computed mass for the offshore region (from Equation (1)) of 5,030 g. As this would be the weight at the initial stage, it seems appropriate to use as the mass for the calculations the equivalent of one-half of the observed loss in mass (202 g) subtracted from the computed initial mass to give a value of 4,828 g. Using these equations, the rate of caloric expenditure per hour was estimated for a 63-cm albacore swimming at 54 cm/s which is the estimated minimum speed a 63-cm albacore can swim and maintain hydrostatic equilibrium, V_{100} (Magnuson 1970; Dotson 1977). Where C_s plus C_m is equal to the total caloric expenditure (C_{total}) during migration, then:

$$\begin{aligned} C_{\text{total}} &= C_s + C_m \\ &= 2.78 \text{ kcal/h} + 0.89 \text{ kcal/h} \\ &= 3.67 \text{ kcal/h}. \end{aligned} \qquad (6)$$

The caloric equivalent of the fat divided by the hourly caloric utilization rate, C_{total}, Equation (6) yields the number of hours that swimming at 54 cm/s could be sustained utilizing this energy source alone and is estimated to be

$$\frac{3{,}272 \text{ kcal}}{3.67 \text{ kcal/h}} = 892 \text{ h or } \sim 37 \text{ days}.$$

The speed and time multiplied together yield the linear distance traveled during this period. This was calculated to be 1,730 km (935 nmi).

Based upon sonic tracking experiments, the average swimming speeds of three albacore 84, 85, and 87 cm in length have been observed to be 95 cm/s during the day and 62 cm/s at night (Laurs et al. 1977). The minimum swimming speed for hydrostatic equilibrium of these fish (V_{100}) is estimated to be about 42 cm/s (Dotson 1977). Assuming the ratio of observed speed (V_0) to minimum speed (V_{100}) to be relatively constant over the size range, then diurnal and nocturnal speeds can be estimated where V_0/V_{100} = 42 cm/s = 2.260 is the multiplier for daylight speeds and (62 cm/s)/(42 cm/s) = 1.575 is the multiplier for night speeds. The result of this estimation is that the daylight and nighttime speeds for a 63-cm albacore are 122 and 80 cm/s, respectively. Assuming equal time spent at each speed, about 6.08 kcal/h are utilized. If the tracking observations are representative of migratory swimming speed, and therefore caloric expenditures, then the fat energy would have been utilized in a period of nearly 22 days and the linear distance traveled would be about 1,960 km (1,060 nmi).

From the nearshore area of capture, the maximum linear distance traveled using the average fat loss of a 63-cm albacore is indicated by points A and B in Figure 1. The two values indicated represent a) 37 days at a minimum speed of 54 cm/s, and b) the estimated diurnal rates of 80 and 122 cm/s for equal portions of 22 days. The interesting result is that both the distances are within the area where the offshore samples with the greater length-mass relationship were collected and compared with the onshore material.

The maximum observed mass difference from the offshore mean of an albacore caught inshore is 999 g or 18% of its body weight for a 65-cm fish (Dotson 1977). Assuming the total weight difference to be fat, at its calculated minimum speed of 54 cm/s, this albacore could have traveled 4,200 km (2,270 nmi) over a period of 90 days utilizing only this fat as an energy source. This would place the fish well out in the mid-Pacific, as shown by point C in Figure 1. Swimming at the estimated day and night speeds of 122 and 80 cm/s for equal parts of the day this fish could travel 4,680 km (2,520 nmi) in 54 days (Figure 1, point D).

These observations, calculations, and hypotheses should indicate some of the potential effects which can be examined in the future, given broad-scale sampling and interest in the migrations of tunas. Fat content is an important indicator of the calories available for migration and/or spawning in fish of sufficient maturity. The importance of immigrants to population assessment in managed fisheries is obvious. Certainly, spawning success and behavior is dependent upon the available caloric stores. For tunas where migration and grazing up to spawning condition may be competitive processes, a thorough examination of the fat level cycles may offer insights into both periodicity and location of the potential spawners. This is an area of minimal understanding in tunas to date. Considering the importance of these processes in the life cycles of tunas, it seems that a certain amount of importance should be placed upon obtaining comprehensive data from several behavioral categories of tunas where inferences could be made about the relation of fat stores and behavior.

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UNDERWATER SOUNDS FROM RIBBON SEAL, *PHOCA (HISTRIOPHOCA) FASCIATA*[1]

Intense downward frequency "sweeps" and broadband "puffing" sounds were recorded underwater in the presence of ribbon seal, *Phoca (Histriophoca) fasciata* Zimmerman 1783. The recordings were made in the waters off Savoonga, St. Lawrence Island, Alaska, on 16, 17, 18, and 23 May 1967.

The seals were encountered in the final ice of the spring made up of windrows of small to moderate floes mixed with brash ice, and with stretches of up to 1 km of open water between. On this ice typically occur adults and pups of a variety of other pinniped species (*Phoca largha, Erignathus barbatus, Pusa hispida,* and *Odobenus rosmarus*), but during the spring of 1967 there was a preponderance of *Histriophoca* in this area. This is reflected in the records of the pinniped harvest for this area (Alaska Department of Fish and Game) which show that *Histriophoca* usually composes less than 2% of the catch, but in 1967 it made up 60% of the harvest and most of the *Histriophoca* were caught during the last half of May. The 1967 underwater recordings showed similar differences, contrasting sharply with previous years when *Erignathus* dominated the underwater sound ambient (Ray et al. 1969).

Relatively little is known of the behavior of *Histriophoca* (cf. Scheffer 1958; King 1964). Breeding assemblages occur on ice that rarely approaches shore (Burns 1970) and other social behavior may mostly occur in the water.

Instruments and Methods

Underwater sounds were recorded with a Chesapeake Instrument Corp.[2] hydrophone system and a Nagra III B tape recorder whose combined response was 50 Hz to 18 kHz (±2 dB, decibels). The sounds were studied by means of a Kay Elemetrics 7029A spectrographic analyzer and time sequences were measured by a Tektronix 565 oscilloscope.

To make the recordings, appropriate *Histriophoca* habitat in the sea ice was located with the aid of Eskimo hunters, and their skin boat was allowed to drift with the ice while the hydrophone was in the water. Only a few of these seals were seen as we approached, and they always submerged and were difficult to find again. However, some of their underwater sweep sounds were loud enough to be audible in air, implying that these seals were not far away.

Taped sequences of 5 to 8 min duration were analyzed from each of nine locations over 4 days of field study. Higher level underwater sounds, presumably from nearby seals, were analyzed and compared with background lower level sounds. Sounds from distant animals were not used for detailed analysis.

As is usually the case with underwater record-

[1]Contribution No. 3753 from the Woods Hole Oceanographic Institution.

[2]Reference to manufacturers does not imply endorsement by the National Marine Fisheries Service, NOAA.

ings, the attribution of these sounds to *Histriophoca* is circumstantial since they are underwater sounds from animals out of sight below the surface. These sounds are unlike sounds attributed to any of the other animals known to inhabit the area: gray whales (Asa-Dorian and Perkins 1967; Cummings et al. 1968; Fish et al. 1974), walrus (Schevill et al. 1966; Ray and Watkins 1975), and the ringed seal and spotted seal (Schevill et al. 1963; Stirling 1973; Ray pers. obs.). The bearded seal, *Erignathus barbatus,* was seen at times in low numbers during May 1967; some of the recordings have a background that we recognize as from *Erignathus,* but we eliminate it because: 1) the *Histriophoca* sounds are very different from the *Erignathus* sounds heard at this season (Ray et al. 1969); 2) in previous years when only *Erignathus* was nearby, none of the *Histriophoca* sounds was heard; 3) *Histriophoca* sounds were heard in the presence of these seals whether *Erignathus* were audible or not; and 4) none of these sounds were heard unless *Histriophoca* were observed in the area.

The recordings were made in a variety of ice conditions and ice is known to produce sounds underwater (Schevill 1966; Watkins and Ray pers. obs.). The seal sounds did not vary with the ice and did not match the kinds of sound we associate with ice.

Underwater Sounds

Two types of underwater sounds were heard in the presence of *Histriophoca:* a relatively intense prolonged downward sweep in frequency and a broadband puffing sound. These calls were heard sporadically, with no obvious pattern to repeated sounds nor to any answering calls. Nearby seals could be heard at least once in 2 min and often there were enough seals in audible range so that when calling was most frequent we recorded 3 to 5 calls in 10 s. Since the seals were out of sight and probably underwater during the recordings, we could not correlate the sounds with behavior.

The sweep sound (Figure 1) varied in frequency from 7 to 0.1 kHz in downward sweeps of 2 to 5 kHz each. Of the 120 sweep sounds measured, all but one could be separated into three length categories (Figure 2), each with somewhat different starting and ending fundamental frequencies:

Short sweeps,	1 s or less,	sweeping from 2000-1750 Hz to 300 Hz.
Medium sweeps,	1.3 to 1.8 s,	sweeping from 5300-2000 Hz to 100 Hz.
Long sweeps,	4 to 4.7 s,	sweeping from 7100-3500 Hz to 2000 Hz.

Short sweeps were common in the background ambient sound, but only a few were heard from nearby seals (16 measured). Midlength sweeps were the ones most often heard from local seals (84 measured), and some of these began with a short segment of sound at constant frequency for the first 0.1 to 0.2 s before beginning the downward frequency sweep (Figure 1). The long sweeps were not particularly abundant but were conspicuous

FIGURE 1.—The midlength sweep sound of *Histriophoca* often has a short portion of constant frequency before it begins to sweep downward in frequency. Analyzing filter bandwidth was 45 Hz. Analyses of short and long sweeps (not figured separately) were generally similar in character to the midlength sweep.

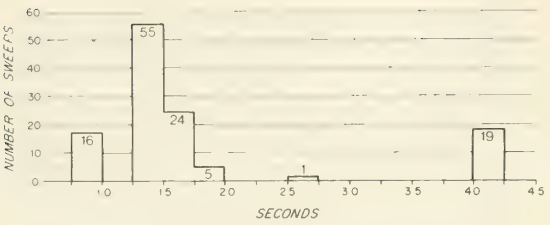

FIGURE 2.—Lengths of 120 sweep sounds from *Histriophoca* separate all but one (at 2.75 s) into three categories.

(19 measured) because of the higher frequency ending. Harmonics (up to 6 or more) were consistently present in the spectrographic analyses of even low-level sweep sounds, and appear to be a result of the pulsed character of the seal sounds (Watkins 1967).

Since we never knew the distance to calling seals, we did not have accurate acoustic source levels for these sounds. Some sweeps overloaded the recording system at the usual gain settings and therefore were received at levels estimated in excess of 40 dB (re 1 volt/dyne·cm^2). Assuming a 60-65 dB source level at 1 m and spherical spreading losses, these very loud sounds were sometimes from animals that were only 15 to 20 m from the hydrophone. Sounds of each type and length category were heard from distant as well as nearby seals so that none of these sounds were characteristic of a particular seal.

A second type of underwater sound which we associate with *Histriophoca* was a broadband puffing sound with frequencies below 5 kHz and lasting a little less than 1 s (Figure 3). This was somewhat reminiscent of some seal respiratory sounds, but it was not audible in air and we could not correlate them with respiratory activity. The puff sounds were 20 to 25 dB lower level than the sweeps.

Discussion

The downward sweeping frequency and pulsed quality of the sounds is characteristic of many underwater calls of other seals: *Erignathus barbatus* (Ray et al. 1969), *Leptonychotes weddelli* (Ray 1967; Schevill and Watkins 1965, 1971), *Pagophilus groenlandica* (Watkins and Schevill in prep.), *Pusa hispida* (Stirling 1973), *Arctocephalus philippii* (Norris and Watkins 1971). Coincident with spring reproductive activities, most of these pinnipeds produce striking underwater acoustic signals and greatly increase their calling. Ovulation normally occurs from mid-April to mid-May in *Histriophoca* and adult males remain sexually potent through early June (Burns[3]). Analogy to these other pinnipeds suggests similar social functions for the underwater sounds of *Histriophoca,* in reproductive and/or territorial behavior.

[3]Burns, J. J. 1969. Seal biology and harvest. Marine Mammal Investigations. Fed. Aid Completion Rep., Alaska Dep. Fish Game 10:1-25.

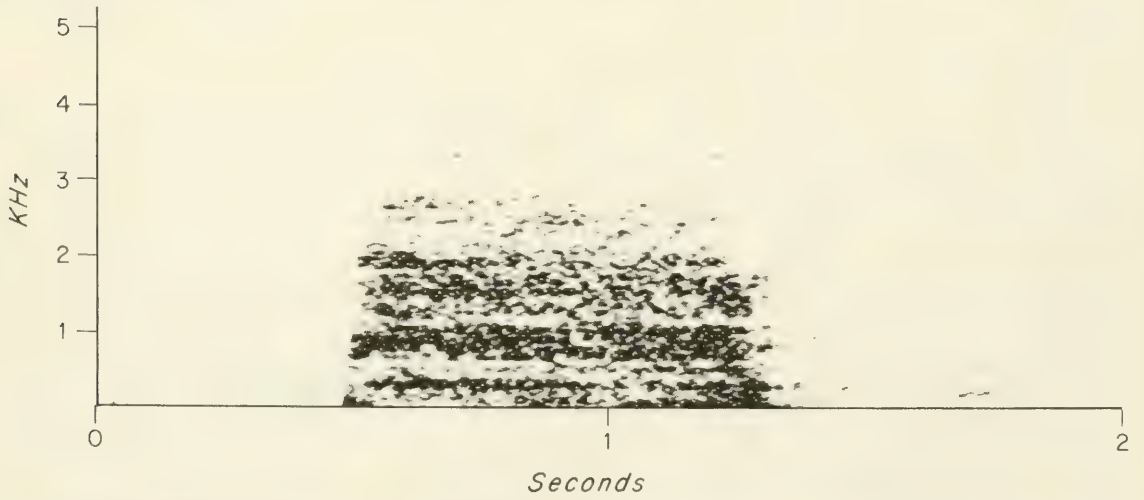

FIGURE 3.—The "puffing" sound of *Histriophoca* is not related to any respiratory activity but is an underwater sound with broadband characteristics that are quite variable. Analyzing filter was 45 Hz.

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OBSERVATIONS ON FEEDING, GROWTH, LOCOMOTOR BEHAVIOR, AND BUOYANCY OF A PELAGIC STROMATEOID FISH, *ICICHTHYS LOCKINGTONI*

Stromateoid fishes (Order Perciformes) occur in either coastal or oceanic regions of the sea. Inhabitants of the latter region are generally rare and sporadic in occurrence, especially as adults. Many of the oceanic species have particular adaptations for pelagic existence (Horn 1975) and their frequent association with floating objects, especially coelenterates (scyphomedusae and siphonophores), is well documented (e.g., Mansueti 1963; Haedrich 1967; Bone and Brook 1973; Horn 1975).

The live capture and successful laboratory maintenance of a juvenile *Icichthys lockingtoni* Jordan and Gilbert (family Centrolophidae), an oceanic fish of the North Pacific, provided the first opportunity to record the feeding, growth, and locomotor behavior of this pelagic stromateoid and, upon the death of the fish, to measure its buoyancy and lipid content (as a factor in buoyancy). In this paper, the laboratory rearing and maintenance of oceanic stromateoids are briefly reviewed, and the adaptive strategy of *I.*

lockingtoni for locomotion and buoyancy in the open ocean is compared with that of another pelagic centrolophid, *Schedophilus medusophagus* Cocco.

Materials and Methods

One *I. lockingtoni* was captured during an open-water skin and scuba diving operation conducted from the RV *Nautilus* in the San Pedro Channel (lat. 33°30'N, long. 118°30'W) off southern California on 24 October 1974. The fish was approached by a scuba diver at a depth of 11 m as it swam slowly beneath a scyphozoan medusa (tentatively identified as a member of the family Pelagiidae) approximately 30 cm in bell diameter. The specimen was captured in a 1-liter jar, placed in a container filled with aerated seawater aboard the ship and transported to the laboratory at California State University, Fullerton, where it was placed in a 95-liter Instant Ocean[1] Tank. Approximately 6 h lapsed between time of capture and placement of the fish in the laboratory tank. Sea temperature at the depth of capture was 15°C and the temperature of the seawater in the tank when the fish was introduced was 13°C. Temperature of the seawater in the tank during the maintenance period ranged from 8.8°C to 22.2°C ($\bar{x}$ ± 1 SD = 14.9 ± 2.2°C) and the salinity from 35.0‰ to 37.5‰ (35.7 ± 2.3‰).

The fish began feeding regularly on 7 November 1974 and was fed daily (except for 8 days, irregularly spaced, when feeding was not possible) by hand with measured amounts of frozen brine shrimp (90% water content). The fish took the food at the surface so that it was possible to keep an accurate record of the amount of food it ingested. The daily diet of frozen brine shrimp ranged in weight from 1.2 to 8 g (0.4–1.4 g dry wt/100 g live wt fish). The feeding rate was based on the amount the fish would consume immediately. Weight and standard length (SL) of the specimen were recorded on 7 November and at irregular intervals throughout the maintenance period by removing the fish in a tray from the tank and placing it on a platform balance beside a metric rule. The weighing and measuring procedure required that the fish be out of water a maximum of 15 s. The conversion of food into fish flesh was obtained by dividing the food intake (dry wt) by the gain in weight of the fish (wet wt) (Hastings and Dickie 1972).

Locomotor behavior was recorded from periodic observations and from analysis of an 8-mm ciné film made of the fish swimming in the tank.

Buoyancy of the specimen was measured immediately after its death (7 April 1975) by weighing it in air and in water of known temperature and salinity. Results were expressed as the percent of the weight in air that the fish weighed in seawater.

After the buoyancy determination the specimen was frozen and later thawed for lipid analysis. Total lipids of the spine, skull, viscera, and flesh (all other tissues) were extracted with chloroform-methanol (2:1, vol/vol) and expressed for each of the four body parts as the percent of total body lipid and as the percent of dry weight of that body part.

Results

The specimen of *I. lockingtoni* became conditioned within 1 wk of capture to take food directly from the hand. Chunks of frozen brine shrimp offered at the surface were quickly approached and usually taken in a single bite. Throughout the maintenance period, the fish occasionally swam upside down, apparently a normal mode of swimming, and sometimes fed in this position. The fish also bit at other available objects in the tank, including human fingers at feeding time, grasping them and then rolling and twisting its body as if to tear free the objects. Vision appeared to be the primary sense used in locating food.

The specimen measured 105 mm SL at the time of capture. On 7 November, when the fish began to feed regularly and the record of food intake and growth was begun, the fish weighed 30.6 g and was 115 mm SL (Table 1). The specimen lived 165 days, until 7 April 1975, when the temperature of the tank increased unexpectedly to 26°C apparently causing death. At death, the fish weighed 54.5 g (78.1% increase over its 7 November weight) and had grown to 168 mm SL (46.1% increase). Its weight peaked on 5 February at 64.6 g then declined to the final value.

During the 151-day period (7 November-7 April), 65.7 g (dry wt) of frozen brine shrimp were ingested by the fish (Table 1). Based on this intake and the weight gain recorded (23.9 g wet wt), the overall conversion factor was 2.7. For the 90-day

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Size, food intake, and food conversion, at cumulative intervals, of *Icichthys lockingtoni* maintained in the laboratory over a 151-day period.

Date	Fish length (mm SL)	Fish weight (g wet wt)	Food intake[1] (g dry wt)	Conversion factor (food intake fish wt gain)
7 Nov. 1974	115	30.6	—	—
22 Nov. 1974	120	33.8	3.8	1.2
14 Dec. 1974	125	36.5	11.7	2.0
4 Jan. 1975	135	43.2	21.2	1.7
5 Feb. 1975	—	64.6	38.9	1.1
7 Apr. 1975	168	54.5	65.7	2.7

[1]Based on 90% water content.

period ending on 5 February when the fish's weight reached a maximum, *I. lockingtoni* ingested 38.9 g of food (dry wt) and gained 34.0 g (wet wt) for a food conversion of 1.1.

The fish swam slowly and continuously most of the time but infrequently hovered in one position. The short (12.6% SL, 168 mm SL), fanlike pectoral fins were the primary propulsive elements when the fish cruised slowly in the tank. Each pectoral fin was flapped in a semirotary manner, alternately to the opposing fin, at approximately 1 stroke/s. At short-term increased speeds, the pectoral fins were held against the body and thrust obtained by sinuous movements of the posterior trunk and caudal region. The small (6.5% SL, 168 mm SL) pelvic fins were actively used during swimming especially in braking and turning. As mentioned, the fish was adept at swimming for short distances upside down and at other attitudes about its longitudinal axis.

The weight of the fish in seawater (20°C, 33‰) immediately after death was 0.36 g or 0.66% of its weight in air (slight negative buoyancy).

Lipids constituted 4.9% of the dry weight of the spine, 10.6% of the skull, 17.0% of the viscera, and 4.4% of the flesh. Spine lipids made up 2.2% of the total body lipids, skull lipids 2.9%, visceral lipids 35.3%, and flesh lipids 59.6%.

Discussion

The stromateoid characteristic of associating with pelagic coelenterates as juveniles is particularly well developed in *I. lockingtoni*. Many of the small (<200 mm SL) specimens captured have been taken with medusae (Fitch 1949; Haedrich 1966; Fitch and Lavenberg 1968). The locomotor behavior and feeding behavior of *Icichthys* recorded in this report are traits well suited for living with medusae. The ability to swim at various attitudes about the longitudinal axis and to hover and maneuver using the paired fins would be advantageous in moving among and avoiding the stinging tentacles of medusae. The grasping of large objects followed by a rolling and twisting of the body appears to be a feeding pattern especially appropriate for tearing chunks from the tentacles and other tissues of coelenterates. Haedrich (1966) reported that the stomachs of *Icichthys* often contain siphonophore remains. A feeding behavior also consisting of grasping objects and twisting the body has been observed (R. L. Haedrich pers. commun.) in two other pelagic centrolophids, *Hyperoglyphe perciforma* (Mitchill) and *Schedophilus medusophagus*.

The food conversion values for *Icichthys* of 2.7 for the 151-day period and 1.1 for the initial 90-day period are comparable to or, in the latter case, more efficient than average total conversions (1.75-2.7) reported by Phillips (1972:19) for brook trout and brown trout fed a variety of diets at temperatures ranging from 8.3° to 15.6°C. The feeding rates of 0.4-1.4% for *I. lockingtoni* were lower than those of 2-3% at which maximum conversion occurred in channel catfish (Tiemeier et al. 1969). Useful comparisons between different experiments and different species are limited since a variety of physical and biological factors influence energy requirements and conversion efficiencies and since food conversions, as calculated here, are less meaningful and often different from caloric conversions (Phillips 1972). The most important result of the present study, however, is that the conversion efficiency of *I. lockingtoni* did change, generally declining with age of the fish (see below).

Limited success has been achieved in maintaining pelagic stromateoids in the laboratory. Maul (1964) recorded rapid growth in two species of centrolophids *Schedophilus* (= *Mupus*) *maculatus* and *Schedophilus* (= *Mupus*) *ovalis*, fed on a diet of shrimp in a large (700-liter) aquarium. The former species increased in weight from 7 to 95 g in 61 days, and *S. ovalis* increased in length from 100 to 198 mm SL over the same period. R. L. Haedrich (pers. commun.) has kept two other centrolophids, *S. medusophagus* and *Hyperoglyphe perciforma*, for 2- to 3-mo periods in small (40- to 100-liter) tanks at Woods Hole Oceanographic Institution. D. Gruber at the Southwest Fisheries Center in La Jolla has hatched and reared a series of larvae of *I. lockingtoni* (E. H. Ahlstrom pers. commun.). One larva that hatched on 12 June 1975 at a notochord length of 3 mm grew to 90 mm SL by 30 August 1975 (80 days).

The rare and sporadic live capture of stromateoids prevents the development of appropriate procedures for long-term maintenance. To date, maintenance trials indicate (pers. obs.; R. L. Haedrich pers. commun.) that the fishes will grow rapidly for short periods but then lose interest in feeding and gradually decline in health, especially as the adult stage is reached when pelagic stromateoids generally change their mode of life and occupy greater depths. The initial growth and high conversion efficiency followed by the reduced growth and lowered efficiency of *I. lockingtoni* are consistent with these observations.

The apparent adaptive strategy for pelagic existence of juvenile *I. lockingtoni* involving locomotor behavior, buoyancy, and lipid content parallels that described (Bone and Brook 1973) for juvenile (85-200 mm SL) *Schedophilus medusophagus* from the North Atlantic. There is no swim bladder in either species in this size range, the lipid content of both is low and both species are slightly negatively buoyant (weight in water 0.35-0.53% of weight in air for *S. medusophagus*). In each case, the pectoral fins are important in generating both thrust and lift.

The two species also appear to undergo similar changes in mode of life as the adult stage (about >200 mm SL) is reached and the fishes become independent of floating objects and occupy greater depths in the water column. Data, particularly on adult *S. medusophagus*, indicate that certain density reducing mechanisms (increase in lipid and water content, decrease in dense tissues, i.e., muscle and bone) are more prominent than in the juvenile stage. Horn (1975) found that a large (285 mm SL) specimen of *S. medusophagus* was neutrally buoyant, swam in a slow, near-anguilliform manner and had relatively small pectoral fins of minor importance in generating thrust and lift. Lipid content in the same specimen was relatively high, especially in the bones (spine 23% and skull 21% lipid by dry wt) (Lee et al. 1975).

Data are yet insufficient on adult *I. lockingtoni* to fully demonstrate parallel strategies in the two species. The relative length of the paired fins of *Icichthys*, however, decrease with age (Haedrich 1966) at a rate and magnitude similar to that in *S. medusophagus*. In addition, the muscles of large (270 mm SL) *Icichthys* are soft and loosely packed as in *Schedophilus*. Data on buoyancy and lipid content of adult *I. lockingtoni* are needed to test the hypothesis.

Acknowledgments

Special recognition is due Wayne S. White who dexterously captured the *I. lockingtoni* and helped identify the medusa with which the fish was associated. I thank Charles F. Phleger for determining the lipid content and the captain and crew of the RV *Nautilus* for facilitating a safe open-water diving operation.

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BODY SIZE AND LEARNED AVOIDANCE AS FACTORS AFFECTING PREDATION ON COHO SALMON, *ONCORHYNCHUS KISUTCH*, FRY BY TORRENT SCULPIN, *COTTUS RHOTHEUS*

Wild coho salmon juveniles, *Oncorhynchus kisutch*, in Washington streams range in fork length (FL) from about 30 mm at the time of emergence from the gravel to 120 mm on migration to the sea. Predation by sculpins, *Cottus* spp., is limited to the smaller salmon; few salmon >45 mm FL have been recovered from the stomachs of sculpins (Patten 1962, 1971a, 1972). Yet, sculpins are capable of eating hatchery reared fall chinook salmon, *O. tshawytscha*, of 60 mm FL (Patten 1971a). Apparently, the reason sculpins do not normally prey on wild coho salmon >45 mm FL is not entirely dependent on the relative sizes of prey and predator.

The present study is on the ability of torrent sculpin, *C. rhotheus*, to prey on coho salmon >45 mm FL, as well as the predator avoidance behavior of coho salmon to torrent sculpins in stream aquaria adjacent to the Cedar River near Ravensdale, Wash., during 1965 and 1966. One experiment indicates the absolute size of coho salmon that can be caught, subdued, and swallowed by a torrent sculpin of a given length. The other suggests that coho salmon previously exposed to torrent sculpins become less susceptible to these predators in future interactions.

Facilities and Procedures

Two related studies—one on predator-prey size relations and the other on the learned predator avoidance ability of coho salmon prey—were conducted in stream and holding aquaria that received water from the Cedar River. The two stream aquaria were 2.4 m long, 0.6 m wide, and 0.6 m high; water depth ranged from 2 to 18 cm. The eight holding aquaria were 34 cm wide, 41 cm long, and 36 cm high; water depth was 18 cm (a more complete description of the experimental facilities is given by Patten 1971b).

Water was gravity fed from a low level dam on the Cedar River to a head box through a flume and then to the aquaria. Each aquarium received a continuous supply of clear water; temperatures in the morning during the study ranged from 4.4° to 12°C.

Torrent sculpins were collected by electrofishing in Soos Creek, King County, Wash., and coho salmon were seined in upper Rock Creek of the Cedar River drainage. It was assumed that the state of hunger of all torrent sculpins was similar, that the coho salmon had little experience with fish predators, and that this experience was similar for all subjects. The assumption for the coho salmon was probably valid because the only other common species of fish at the seining site was the shorthead sculpin, *C. confusus*—a relatively nonpredaceous species of fish (unpubl. studies of author). Furthermore, the few individuals of the shorthead sculpin observed were small.

The effect of predator-prey length relations on predation was determined from 23 tests where six coho salmon of a given length group were available to four torrent sculpins of a given length group (Table 1) for 4 days. The test procedure was to collect torrent sculpins the first day and place them in a holding aquarium without food; on the second day, coho salmon were collected and six individuals within 5 mm of a given length were placed in a holding aquarium; on the third day, four torrent sculpins within 5 mm of a given length were introduced into the holding aquarium containing the coho salmon; 4 days later, the number of coho salmon eaten was recorded and the experimental fish were discarded. The largest available size group of torrent sculpins used was 120 mm total length (TL).

TABLE 1.—Results of 23 tests where six coho salmon of a length group were subjected to predation by four torrent sculpins of a length group. Predation on one or more coho salmon is denoted by P and no predation by N.

Total length of sculpin (mm)	Fork length of salmon (mm)						
	40	50	60	70	80	90	100
60	–	P	N	–	–	–	–
80	P	P	P	N	–	–	–
80	–	P	N	–	–	–	–
100	–	–	P	P	N	–	–
100	–	–	P	N	–	–	–
100	–	–	–	N	–	–	–
120	–	–	P	P	P	N	N
120	–	–	–	–	N	N	N
120	–	–	–	–	P	–	–

The ability of coho salmon to learn to evade predation was tested by comparing the relative survival of naive coho salmon (those which had not been exposed to torrent sculpin predators) with coho salmon conditioned to predation by the torrent sculpin. Coho salmon were conditioned by placing 20 individuals into a stream aquarium with eight torrent sculpins. Some of those that had survived a 48-h association with torrent sculpins

were maintained in holding aquaria without torrent sculpins for 24 h before being subjected to predation in test conditions. Two types of test groups, each consisting of 20 coho salmon (per stream aquarium), were used. In the naive group, all coho salmon were naive; in the naive and conditioned group, 10 naive and 10 conditioned fish were tested together.

The procedure for testing naive coho salmon was to collect torrent sculpins and place them in holding aquaria without food; on the second day, coho salmon were collected and 20 individuals, 37 to 42 mm FL, were placed in each stream aquarium; on the third day, 10 torrent sculpins, 83 to 127 mm TL, where lengths averaged about 100 mm per test group, were transferred from the holding aquarium to each stream aquarium. Forty-eight hours later, the surviving coho salmon were counted and experimental fish were discarded.

The procedure for testing the naive and conditioned group of coho salmon was similar to the foregoing test procedure except that on the second day, 10 naive coho salmon were collected and placed in each stream aquarium with 10 conditioned coho salmon. The tip of a ventral fin of the conditioned coho salmon was clipped at the time they were introduced into the stream aquarium to allow them to be recognized at the end of the test. Thus, if there was an adverse effect from clipping, it would be on the group with the greater expected survival. Eight replicate tests were made on each of the two conditions.

Length Relation

The experimental procedure placed the coho salmon in close proximity to torrent sculpins for a prolonged period to enhance the possibility of predation. Torrent sculpins responded to this opportunity by preying on larger coho salmon than has been observed in nature (Table 1). The maximum size of coho salmon a torrent sculpin is capable of preying upon is probably limited by the physical size of a coho salmon that a torrent sculpin can catch, subdue, and swallow. While the swimming ability is probably greater for larger coho salmon, this may not be too important because predation by torrent sculpins is accomplished by ambush rather than by pursuit. Torrent sculpins under natural conditions rarely eat coho salmon 40 to 80 mm FL, indicating that some factor of coho salmon behavior must decrease their susceptibility to predation.

Predator Avoidance Response

The average survival of the naive group consisting only of naive fish was 45.5%; within the naive and conditioned group, consisting of conditioned and naive coho salmon tested together, the naive fish had a 71% survival, and the conditioned coho salmon had a 75% survival. Cumulative chi-square tests of homogeneity showed no significant differences within the naive test group or within the naive and conditioned group (Table 2). The Z test showed no significant difference between the conditioned and naive coho salmon that were tested together ($Z_{P0.05} = +0.53 < 1.645$). There was, however, a significant difference between the group consisting of naive coho salmon only and the group consisting of naive plus conditioned coho salmon ($Z_{P0.05} = +5.29 > 1.645$).

Mortalities of coho salmon were significantly reduced by conditioning; also, naive fish tested with conditioned fish behaved as conditioned fish. The results of these tests are probably due to rapid conditioning of the coho salmon and a transferable predator avoidance reaction. Rapid conditioning was evident because conditioning of fish to a stimulus other than predators is usually accomplished only after many trials. Conditioning coho salmon to evade predation by exposing them to torrent sculpins probably reinforces a strong innate avoidance behavior. In another case, rapid conditioning of sockeye salmon, *O. nerka,* to evade predation by rainbow trout, *Salmo gairdneri,* has been demonstrated by Ginetz and Larkin (1976). Experiments by Russians have shown that certain fishes, including the chum salmon, *O. keta,* increased their ability to evade predation after a 2- to 4-day training period with predators (Kanid'yev et al. 1970).

TABLE 2.—Comparative survival of two groups of coho salmon that were exposed to predation by the torrent sculpin. One group consisted of naive fish only and the other consisted of naive and conditioned coho salmon combined. The initial number of coho salmon per group per stream aquarium was 20.

Naive group		Naive and conditioned group			
		Naive		Conditioned	
No. of fish	Survivors	No. of fish	Survivors	No. of fish	Survivors
20	6	10	7	10	9
20	12	10	9	10	10
20	12	10	6	10	6
20	7	10	7	10	9
20	8	10	5	10	8
20	10	10	7	10	6
20	12	10	9	10	7
20	6	10	7	10	5

A transferable predator avoidance reaction may account for the conditioned and naive coho salmon acting as a homogeneous group in the present study. Conditioned coho salmon had learned to avoid torrent sculpins through some unknown mechanism. Apparently the naive fish behaved as conditioned individuals through visual clues resulting in mimicry. O'Connell (1960) noted mimicry in sardines in a conditioned response experiment where unconditioned replacement fish performed in unison with the school of conditioned fish from the first trial. Kanid'yev et al. (1970) indicated that the consensus of Russian workers was that sight played the main role in developing the predator avoidance reaction and that reinforcement is maximal for fish that are observers.

Sculpins commonly cohabit streams with and prey on young salmon. Growth of salmon to a size too large for sculpins to successfully prey on effectively removes them from this predator predation. The maximum size of coho salmon that a torrent sculpin can catch and eat in laboratory conditions is much larger than those that are normally preyed upon in nature. This indicates that although growth is effective in limiting torrent sculpin predation on coho salmon, other factors are equally important. Among salmon, the coho has a well-developed innate predator avoidance response (Patten 1975). The response apparently can be reinforced by experience with fish predators and this conditioning probably increases their early survival in streams.

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DESCRIPTION OF MEGALOPA OF SNOW CRAB, *CHIONOECETES BAIRDI* (MAJIDAE, SUBFAMILY OREGONIINAE)

Chionoecetes bairdi Rathbun, a brachyuran crab, occurs on the continental shelf from Puget Sound in Washington State, northward into the Bering Sea, and westward along the Aleutian Islands. The species has been taken as deep as 474 m (Garth 1958), but adults commonly occur at depths less than 190 m. *Chionoecetes bairdi* may be quite abundant in inshore areas throughout its range and has become an important subsistence and commercial species because of its large size and accessibility. It supports an extensive fishery in the Bering Sea and Gulf of Alaska for three nations—the United States, the Soviet Union, and Japan.

The range of *C. bairdi* overlaps that of three other species of *Chionoecetes: C. tanneri* Rathbun, *C. angulatus* Rathbun, and *C. opilio* (O. Fabricius). *Chionoecetes tanneri* ranges from Mexico north to the State of Washington, and commonly occurs between 370 and 1,630 m on the outer slopes of the continental shelf (Garth 1958). *Chionoecetes angulatus* occurs throughout the range of *C. bairdi*, but *C. angulatus* occurs on the lower slopes of the shelf edge between 730 and 2,980 m (Garth 1958). *Chionoecetes opilio* occurs only in the Bering Sea, and its distribution is often sympatric with *C. bairdi*. Two other species of *Chionoecetes* occur in the western Pacific Ocean,

C. japonicus (Rathbun) and *C. opilio elongatus* Rathbun.

Since *C. bairdi* has become commercially important, its biology and distribution are receiving more attention. Descriptions of the larvae for *C. bairdi* and *C. opilio* are important because both are taken commercially and their distribution overlaps. Haynes (1973) described prezoeae and stage I zoeae of *C. bairdi* (and *C. opilio*), but stage II zoeae and megalopa have not been described.

In this paper we describe megalopa of *C. bairdi* and compare them with megalopa of *C. opilio* (Motoh 1973) and *C. opilio elongatus* (Kurata 1963b)—the only other *Chionoecetes* species for which the megalopal stages have been described.

There seems to be some lack of consistency in the literature concerning the singular and plural of the megalopal stage. The original singular was called megalops, because of the large and prominent eyes. Many authors (e.g., Kurata 1963a, b; Makarov 1967; Motoh 1973) have changed this to megalopa for both singular and plural. Others (e.g., Hart 1960; Poole 1966) have latinized megalopa in the plural to megalopae. In this manuscript both singular and plural of the megalopal stage will be referred to as megalopa since this is more widely accepted.

Methods and Materials

About 50 larvae[1] of *C. bairdi* were taken from Fish Bay near Sitka, Alaska, at lat. 57°22′N, long. 135°33′W on 14 April 1971. They were caught with 70-cm-diameter nylon bongo nets towed 8 to 9 m below the surface; mesh sizes of the nets were 0.505 and 0.333 mm. The larvae were held in a 3-liter aquarium supplied with continuous-flowing filtered seawater. The aquarium was transferred from the research vessel to the laboratory on 19 April. The water temperature fluctuated between 8° and 10°C on the vessel and 6.3° and 6.9°C in the laboratory. The *C. bairdi* larvae fed upon other zooplankton caught during the same tow until that food was gone. By then, it appeared all the larvae were at the megalopal stage, and we began feeding them finely chopped herring. Some megalopa were preserved on 19 April in 5% formaldehyde and seawater. Their identification as *C. bairdi* was confirmed by raising the remaining megalopa to the juvenile stage (maximum carapace width 13.9 mm) and comparing them with the juvenile morphology described by Garth (1958).

Megalopal larvae identical morphologically to those we had raised were collected in a vertical plankton haul on 21 May 1973, at the entrance to Resurrection Bay south of Seward, Alaska, at lat. 59°48′N, long. 149°30′W. These specimens were dissected and used as the basis for our illustrations of morphology, appendage setation, and other characteristics.

Illustrations (Figure 1) were prepared with the aid of a camera lucida. An ocular micrometer was used to measure body dimensions of nine of the preserved specimens. The measurements were 1) carapace length (two measurements had to be taken because the rostral tip was often damaged—straight-line distance from rostral tip to posterior median margin of carapace and straight-line distance from the notch between rostral and preorbital spine to posterior median margin of carapace); and 2) carapace width (straight-line distance between widest part of carapace).

To compare our description of megalopal larvae of *C. bairdi* with descriptions of megalopa of other species in the genus, we used our collections from the Chukchi Sea and descriptions by Motoh (1973) for *C. opilio* and descriptions by Kurata (1963b) for *C. opilio elongatus*.

Description of Megalopa

Carapace length 3.12 to 3.48 mm (mean 3.30 mm) inclusive of rostrum and 2.60 to 2.80 mm (mean 2.73 mm) from rostral notch. Carapace width 1.80 to 2.12 mm (mean 1.97 mm).

Carapace triangular shaped and bears seven major processes (Figure 1a-c). Anterior rostral region bears three sharp spines, two preorbital and one rostral. Rostral spine three times length of preorbital spines (measuring from rostral notch) and points ventrally. Frontal and rostral region slightly depressed. Pair of anterolateral spines separated by thin median ridge. Pair of cardiac dorsolateral spines sweep slightly posteriorly. Minute but conspicuous lateral spines occur in region of pterygostomial-branchial ridge. Small ridge along posterolateral margin of carapace bears a wartlike protuberance medially, directly above proximal end of abdomen. Eyes stalked.

[1]The specimens preserved 14 April were lost and could not be examined to determine their stage of development. We believe that they were stage II zoeae or megalopa or a combination of both.

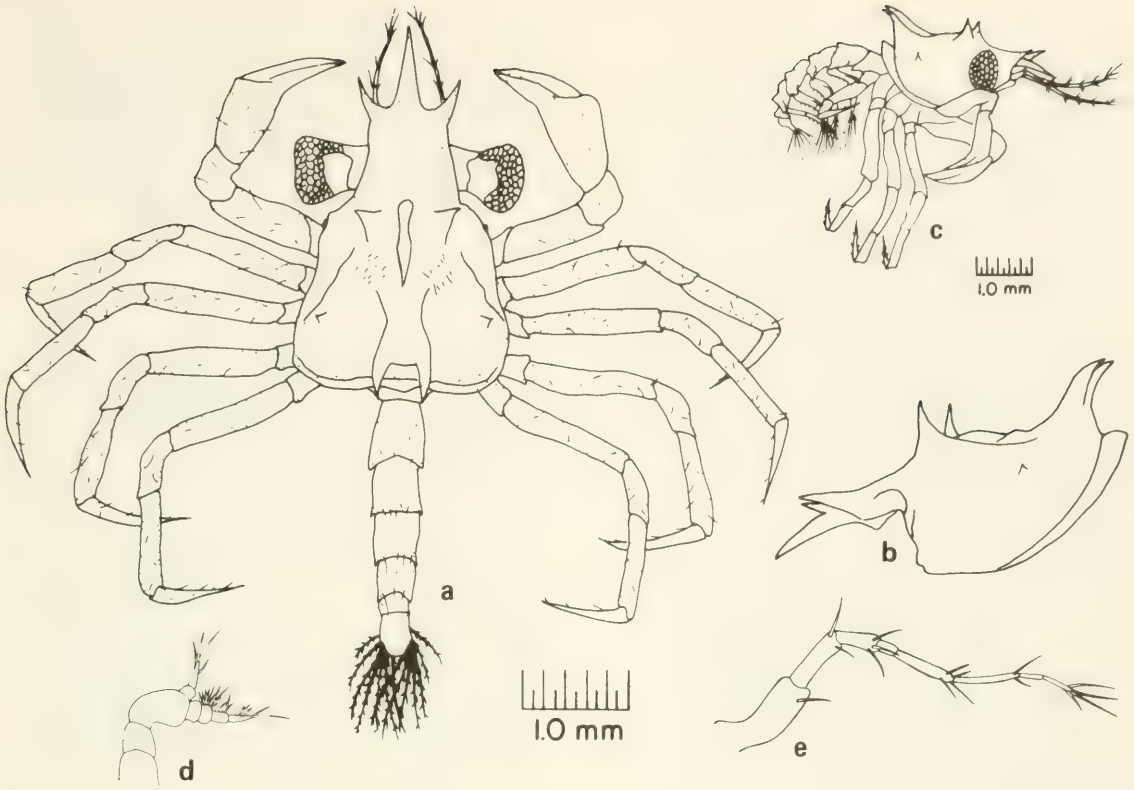

FIGURE 1.—Megalopa of *Chionoecetes bairdi;* antennule and antenna from right side of specimen (a) dorsal view of entire specimen; (b) lateral view of carapace; (c) lateral view of entire specimen; (d) antennule; (e) antenna.

ANTENNULE (Figure 1d)—Three-segmented peduncle has terminal pair of segmented rami. Smaller ramus has two segments. Distal segment has four setae, proximal shorter segment naked. Second terminal ramus has four segments. Number of setae per segment, beginning distally, 5, 3, 10, and 0.

ANTENNA (Figure 1e)—Antenna has eight segments. Setation formula is 4, 0, 2, 4, 0, 3, 2, and 1. Setae located on distal ends of segments.

MANDIBLE (Figure 2a)—Mandibular palp has three segments. Distal segment has about 10 setae; middle and proximal segments naked.

MAXILLULE (Figure 2b)—Endopodite has one hook-shaped segment with two terminal setae. Basipodite has 20-23 coarse plumose setae. Smaller coxopodite has 13-16 coarse plumose setae.

MAXILLA (Figure 2c)—Exopodite (scaphagnathite) outer margin lined with 38 plumose setae. One endite naked and ends in a point. Two endites heavily bifurcated. Lobes of basal endite distally bear 10 and 8 plumose setae, respectively, and lobes of coxal (proximal) endite bear 6 and 10 plumose setae.

FIRST MAXILLIPED (Figure 2d)—Epipodite has eight long hairs. Exopodite is two segmented with six heavily plumose setae; setation formula is 5 and 1. Broad endopodite has three spines on distal end. Basal endite bilobed with 22-29 plumose setae on larger lobe and 11-14 plumose setae on smaller.

SECOND MAXILLIPED (Figure 2e)—Epipodite has three hairs. Exopodite has two segments with five heavily plumose setae on distal segment. Endopodite has four segments; setation formula 9, 4, 1, and 1.

THIRD MAXILLIPED (Figure 2f)—Epipodite well developed with several nonplumose hairs. Exopodite two segmented with five terminal setae. Endopodite has five large segments with numerous spines on all segments; setation formula 8, 15-17, 8-10, 8, and 30-34.

PEREIOPODS (Figures 1a, 2g)—Pereiopods

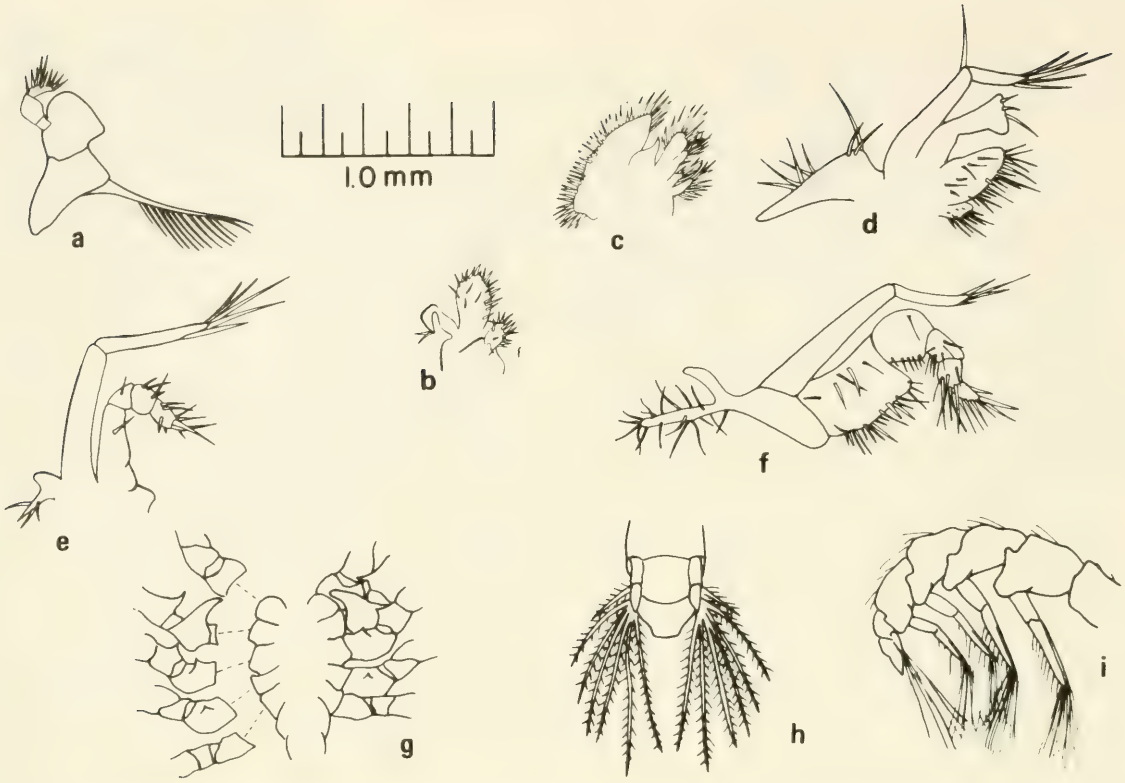

FIGURE 2.—Mouthparts from right side of megalopa of *Chionoecetes bairdi* (a) mandible; (b) maxillule; (c) maxilla; (d) first maxilliped; (e) second maxilliped; (f) third maxilliped; (g) ventral view of sternum and pleopod attachment; (h) ventral view of telson and uropods; (i) lateral view of abdomen.

closely resemble those of adult. Coxopodite and basipodite spines, one each, located ventrally on chelipeds and ambulatory legs except for fourth leg. First ambulatory leg spines especially long. Cheliped and third ambulatory leg spines minute. Dactylopodites of ambulatory legs one, two, and three have conspicuous spine projecting from tip.

ABDOMEN AND TELSON (Figure 2h, i)—Abdomen six segmented. Sixth segment and telson small. No spines present. Segments two through five have long setae on dorsal surface.

PLEOPODS (Figure 2i)—Pleopods present on abdominal segments two through five. A single-segmented endopodite (not shown in figure) arises from proximal segments of each pleopod. Endopodites have four hooked setae on distal end of first three pairs of pleopods and three hooked setae on distal end of last pair of pleopods. Exopodites of pleopods two and three have variable numbers of plumose setae, 15 through 18. Exopodites of pleopods four and five have 17 and 15 plumose setae, respectively.

UROPODS (Figure 2h)—Uropods two segmented and have seven plumose hairs arising from each distal segment.

How to Distinguish Megalopa of *Chionoecetes bairdi, C. opilio,* and *C. opilio elongatus*

Megalopa of *C. bairdi* are similar to megalopa of *C. opilio* and *C. opilio elongatus* in major carapace spination and size. The characteristics which separate these species can be determined without dissection. The four most useful characteristics are: 1) *C. bairdi* has a minute lateral spine in the region of the pterygostomial-branchial ridge while the others do not (see Kurata 1963b; Motoh 1973); 2) *C. bairdi* has a more pronounced ridge along the posterior margin of the carapace than *C. opilio* and *C. opilio elongatus* (Kurata 1963b; Motoh 1973); 3) the rostral spine of *C. bairdi* is three times the length of the preorbital spines, whereas the rostral spine on *C.*

opilio is 1.5 to 2.0 times the length of the preorbitals (from our samples from Chukchi Sea); and on *C. opilio elongatus* all three spines are nearly the same length (Kurata 1963b); 4) *C. bairdi* has a rudimentary spine immediately posterior to each eye; in *C. opilio* and *C. opilio elongatus* this spine, though still minute, is quite conspicuous.

Key to Megalopa of Some Common Brachyuran genera of the Northwest

The following key is to provide a means of identification of some common Brachyura megalopa of the northwest to the generic level. As only characteristics which can be determined without dissection have been used, the key should be used for preliminary sorting. The present state of knowledge of these megalopa comes from six sources (i.e., Hart 1960; Kurata 1963a, b; Poole 1966; Makarov 1967; Motoh 1973). Key modified after Makarov (1967).

A. Carapace bears dorsal spines
  B. Posterior part of carapace bears one spine ..... *Hyas; Oregonia; Cancer*
  B′. Posterior part of carapace bears two spines ..... *Chionoecetes*
A′. Carapace bears no dorsal spines
  B. Angles of posterior margin of abdominal somite 5 reach beyond somite 6 ..... *Telmessus*
  B′. Angles of posterior margin of abdominal somite 5 reach to middle of somite 6 ..... *Erimacrus*

Acknowledgments

Funding in partial support of this project was made available through U.S. Department of Commerce (NOAA) contract no. 03-5-022-56 to H. M. Feder, Institute of Marine Science, University of Alaska, Fairbanks.

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A COMPARTMENTALIZED SIMULATION MODEL OF THE SOUTHERN NEW ENGLAND YELLOWTAIL FLOUNDER, *LIMANDA FERRUGINEA*, FISHERY

MICHAEL P. SISSENWINE[1]

ABSTRACT

A compartmentalized simulation model of the Southern New England yellowtail flounder, *Limanda ferruginea*, fishery was developed. The population was divided into 10 age-groups, each of which was subdivided into 7 size categories. The model simulated discard mortality as well as natural mortality and fishing mortality. Fishing and discard mortality rates depended on the level of fishing and on gear and market selection factors. Both linear and density independent stock-recruitment functions were considered. Seasonal variations in growth and exploitation were incorporated into the model. The influence of fluctuation in temperature on recruitment and growth was also simulated. The model using a linear stock-recruitment function accounted for 85.5% of the variability in the yield of the fishery for 1943–65; with a density independent stock-recruitment function, the model explained 83.2% of the variability in yield for the same period.

The linear stock-recruitment model was used to investigate the response of the fishery to alternative fishing strategies. Substantial increases in the past yield of the fishery were indicated by the model when fishing effort was concentrated during the second half of the year and when fishing effort and discard mortality were reduced.

This paper describes a compartmentalized simulation model of the Southern New England yellowtail flounder, *Limanda ferruginea* (Storer), population. There is evidence that production of the Southern New England yellowtail flounder population is influenced by environmental temperature (Sissenwine 1974). The model is intended to demonstrate the feasibility of predicting catch under fluctuating environmental conditions based on the rate of exploitation. The model shares many of the characteristics of Walters' (1969) "generalized computer simulation model," which incorporates growth, fishing and natural mortality, and a stock-recruitment relationship, and also incorporates several additional features. These features include 1) temperature dependent growth and recruitment, 2) growth and fishing mortality rates which vary seasonally, and 3) age-groups subdivided into size categories.

More than 600 thousand metric tons of yellowtail flounder valued at over $120 million have been landed in Southern New England and New York since the onset of fishing in the late 1930's. The magnitude of the fishery has stimulated numerous quantitative investigations. Royce et al. (1959), Lux (1964, 1969a), Brown and Hennemuth,[2] Brown,[3] and Parrack[4] reported catch and fishing effort data for each of the three major fishing grounds (Lux 1963) since 1943. Until recently, most of the catch has been from the Southern New England ground. Catch and fishing effort data were used by Sissenwine (1974) to estimate the annual recruitment and equilibrium catch produced by the Southern New England ground for 1944–65. The equilibrium catch and recruitment were shown to be highly correlated with the atmospheric temperature record at Block Island, R.I. Lux and Nichy (1969) determined the growth rate of the yellowtail flounder. Lux (1969b) and Pitt (1971) calculated the length–weight and length–fecundity functions of the species, respectively. Mortality rates of the yellowtail flounder were estimated by Lux

[1]Graduate School of Oceanography, University of Rhode Island, Kingston, RI 02881; present address: Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[2]Brown, B. E., and R. C. Hennemuth. 1971. Assessment of the yellowtail flounder fishery in Subarea 5. Int. Comm. Northwest Atl. Fish., Res. Doc. 71/14, Ser. No. 2599, 57 p.

[3]Brown, B. E. 1972. Current status of the yellowtail flounder fishery in ICNAF Subarea 5 – January, 1972. Int. Comm. Northwest Atl. Fish., Res. Doc. 72/23, Ser. No. 2174, 18 p.

[4]Parrack, M. L. 1973. Current status of the yellowtail flounder fishery in ICNAF Subarea 5. Int. Comm. Northwest Atl. Fish., Res. Doc. 73/104, Ser. No. 3067, 3 p.

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FISHERY BULLETIN: VOL. 75, NO. 3, 1977.

(1969a), Brown and Hennemuth (see footnote 2), and Penttila and Brown.[5]

Some of the research cited above is recorded only in unpublished documents. Any information extracted from these reports must be considered as preliminary. Accordingly, the work reported in this paper was primarily based on the published literature.

Catch data used in this paper include both domestic and foreign landings of yellowtail flounder but exclude the industrial catch. All effort data are expressed in standard days fished as defined by Lux (1964).

DESCRIPTION OF THE MODEL STRUCTURE

A diagram representing the compartments and activities of the system is shown in Figure 1. Since yellowtail flounder greater than 10 yr of age are seldom encountered, fish were divided into 10 age-groups. Certainly, the length of individuals within each age-group is not uniform. Therefore, each age-group was subdivided into seven size categories in which all fish were assumed to be of a uniform length. The number of size categories was limited to seven in order to minimize computer cost. The level (number of fish) of each of the 70 age–size compartments is denoted by $N_{i,j}$ where i indicates the age-group and j the size category. Another attribute of each compartment is its mean length, denoted by $L_{i,j}$ with i and j defined in the same manner.

The yield of the fishery in weight (Y_w) and number of fish (Y_n) landed annually are attributes of the yield compartment. Total fecundity of the population during each spawning season is P_e (number of eggs in the egg compartment).

The important activities affecting the system are: 1) fishing which results in a continuous transfer of fish from age–size compartments to the yield compartment and results in some non-productive mortality (discard mortality) since not all fish captured are actually landed (Brown and Hennemuth see footnote 2); 2) natural mortality which results in a continuous decay of each age–size compartment and loss of fish from the system; 3) aging which results in a discrete advancement

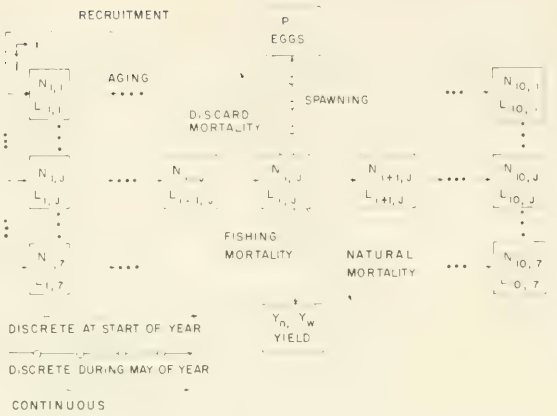

FIGURE 1.—Compartments representing a fish population. Three dots (. . .) indicate additional compartments. The age-group is indicated by i and the size category by j. $N_{i,j}$ is the number of fish in the jth size category of age-group i, and $L_{i,j}$ is the mean length of the fish of the same compartment. Each compartment (only shown for (i,j)) undergoes continuous loss due to fishing, discard, and natural mortality. Losses due to fishing mortality are added to the yield compartment. At the beginning (or end) of each year, aging occurs, advancing each compartment to the next higher age-group, retaining the same value of j. Recruitment to age-group 1 also occurs at the beginning of each year as a function of the previous year's egg production. Spawning occurs during May of each year (only shown for (i,j)) with egg production a function of the number and size of fish in each compartment.

of fish to the next higher age-group (retaining the same value of j) at the beginning of each year; 4) spawning which is the discrete production of eggs (P_e) during May (Bigelow and Schroeder 1953) of each year; 5) recruitment which is represented as the discrete addition of individuals to the youngest age-group of the model at the beginning of each year according to the magnitude of P_e during the previous year; and 6) growth which results in a continuous increase in $L_{i,j}$.

The dynamic system briefly described above was simulated by a FORTRAN program using finite difference approximation. Details of each activity regulating the system are presented below. The variables used in the model are defined in Table 1.

Fishing, Discard, and Natural Mortality

Each age–size compartment is subject to mortality at a rate proportional to the number of fish of the compartment; that is,

[5]Penttila, J. A., and B. E. Brown. 1972. Total mortality rates for two groups of yellowtail flounder estimates from survey cruise data from ICNAF Subarea 5. Int. Comm. Northwest Atl. Fish., Res. Doc. 72/22, Ser. No. 2713, 14 p.

TABLE 1.—List of variables of yellowtail flounder, *Limanda ferruginea*, model.

Variable	Description
$N_{i,j}$	Number of fish in size category j of age-group i
$L_{i,j}$	Length of fish in size category j of age-group i
Y_n	Yield of fishery in number of fish
Y_w	Yield of fishery in weight of fish
P_e	Annual egg production of stock
W	Weight of fish as function of length
Fe	Fecundity of fish as function of length
Z	Instantaneous total mortality rate
D	Instantaneous discard mortality rate
F	Instantaneous fishing mortality rate (excluding discard mortality)
M	Instantaneous natural mortality rate
G	Instantaneous gear mortality rate ($G = F + D$)
f	Instantaneous rate of fishing
t	Time
P_1	Relative gear effectiveness as function of length
P_2	Probability of landing a captured fish as function of length
P_4	Probability of a fish being mature as function of length
T	Index of temperature
k	Growth rate coefficient of von Bertalanffy equation
T_r	Recruitment–temperature factor as function of temperature
T_g	Growth–temperature factor as function of temperature
R	Annual recruitment to age 1

$$\frac{d(N_{i,j})}{dt} = -(F + D + M) \cdot N_{i,j} \qquad (1)$$

where F, D, and M are the instantaneous fishing, discard, and natural mortality rates, respectively, and t is time in years. Total mortality of fish greater than 10 yr old was assumed. Very few fish reach this advanced age. Lux (1964) reported that fish discarded at sea suffered a high mortality rate. In the model, all discarded fish were assumed lost. The yield rate, in number of fish and biomass, contributed by each compartment is

$$\frac{d(Yn)}{dt} = F \cdot N_{i,j} \qquad (2)$$

and

$$\frac{d(Yw)}{dt} = F \cdot N_{i,j} \cdot W(L_{i,j}) \qquad (3)$$

where $W(L)$ is a function relating the weight of a fish to its length. This function assumes the usual form,

$$W(L) = c_1 \cdot L^{c_2}. \qquad (4)$$

The letter c with a numerical subscript is used throughout the paper to denote constants. The total yield rate is obtained by summing $d(Yn)/dt$ and $d(Yw)/dt$ for all age–size compartments.

The mortality rate inflicted by fishermen ($F + D$) on the yellowtail flounder population is assumed to be proportional to the instantaneous annual rate of fishing (f) for fish which are fully vulnerable. This mortality is called the gear mortality (G),

$$G = F + D = q \cdot f \qquad (5)$$

where q is the catchability coefficient. The number of days fished annually is determined externally to the model and acts as a driving variable. Natural mortality was assumed to decrease with age until maturation and then remain constant through the rest of the life span.

In order to approximate the seasonality of fishing, the instantaneous rate of fishing is estimated by multiplying the total number of days fished annually by quarterly effort adjustment factors (c_3, c_4, c_5, and c_6) where the average value of these factors is 1.

Yellowtail flounder first become available to trawl gear on the Southern New England ground in about 1 yr (Brown and Hennemuth see footnote 2), but they are not captured commercially until they have grown to the minimum size retained by the fishermen's nets, $L_{g\min}$. Some fish continue to escape the nets because of their small size until they have grown to the length at which the gear obtains its maximum effectiveness, $L_{g\max}$. It is assumed that the relative effectiveness of the gear from fish with a length between $L_{g\min}$ and $L_{g\max}$ can be calculated by linear interpolation. Accordingly, the relative effectiveness of the gear, P_1, is defined as follows:

$$P_1 \begin{cases} (L - L_{g\min})/(L_{g\max} - L_{g\min}) \\ \quad \text{for } L_{g\min} \leq L \leq L_{g\max} \\ 0 \text{ for } L < L_{g\min} \\ 1 \text{ for } L > L_{g\max} \end{cases} \qquad (6)$$

where L is the length for which P_1 is applied.

Since not all of the fish captured are large enough to be marketed (for economic and technological reasons), the probability of landing a captured fish (P_2) as a function of its length must be calculated. Let $L_{m\min}$ be the minimum length landed by the fishermen and $L_{m\max}$ be the length at which all fish are landed. Note that the determination of the marketability of each fish is made by the fishermen on the decks of their vessels. Therefore, a gradual transition from total unacceptability to total acceptability as L increases is expected. Again applying linear interpolation,

$$P_2 \begin{cases} (L - L_{m\min})/(L_{m\max} - L_{m\min}) \\ \quad \text{for } L_{m\min} \leq L \leq L_{m\max} \\ 0 \text{ for } L < L_{m\min} \\ 1 \text{ for } L > L_{m\max}. \end{cases} \quad (7)$$

Using Equations (5), (6), and (7); G, F, and D are calculated as follows for fish of any length:

$$G = q \cdot f \cdot P_1 \quad (8)$$
$$F = q \cdot f \cdot P_1 \cdot P_2 \quad (9)$$
$$D = q \cdot f \cdot P_1 \cdot (1 - P_2). \quad (10)$$

Since G, F, and D vary with L and f, they are time dependent functions.

Aging

The aging process of yellowtail flounder is simulated by advancing individuals of each age–size compartment to the next higher age-group within the same size category.

Growth

The mechanism used in the model to simulate growth was based on the von Bertalanffy growth function. The von Bertalanffy function can be expressed in many forms, but the following is most applicable to this study:

$$L = L_m + (L_0 - L_m) \cdot e^{-kt} \quad (11)$$

where L_m is the maximum length obtained by the fish of the population, L_0 is the length of a fish at the beginning of a time interval of duration t, k is the growth rate coefficient that applies during the interval, and L is the length obtained by the end of the interval. The derivative of Equation (11) is identical to the growth equation deduced by von Bertalanffy (1938).

A single value of L_m is usually assumed for an entire population. In the model, differences in the mean length of size categories are maintained by assigning a unique maximum value to L for each size category ($L_{m1}, L_{m2}, \ldots, L_{m7}$). Fish are distributed among the size categories in the following manner. Assume L_m is a normally distributed random variable with mean L_{m4} and standard deviation s_m. For $G_1, G_2, \ldots, G_7$, the portion of the population in each size category respectively (in the absence of fishing), the range of values of L_m included in each size category can be determined from a standard normal table. The mean value of L_m for the jth size category (L_{mj}) is obtained by integrating the product of the normal density function and the random variable L_m over the range of values of L_m included in the size category and then dividing the result by G_j.

Taylor (1962) showed that k of the von Bertalanffy function was related to water temperature for a number of species, and there is evidence (which is discussed later in this paper) that this is also true for the Southern New England yellowtail flounder. The influence of temperature on k is simulated by adjusting k by a multiplicative growth–temperature factor, T_g, defined as

$$T_g = 1 + c_{14} \cdot (T - \bar{T}) \quad (12)$$

where T is an index of temperature and $\bar{T}$ is the average value of the index over the total period for which data are available. T is an exogenous variable of the model.

Different values of k (k_1, k_2) were necessary to describe the growth of yellowtail flounder less than and greater than 2 yr old (Lux and Nichy 1969). Seasonal variations of growth were incorporated into the model by multiplicative quarterly growth factors K_1, K_2, K_3, K_4 (with an average value of 1.0). The length of age–size compartment i,j after an interval of time t is calculated according to Equation (11) using the length of the compartment at the beginning of the interval L_{mj}, and k as follows:

$$k = k_a \cdot k_n \cdot T_g \quad (13)$$

where n indicates the quarter of the year and a indicates age less than or greater than 2 yr.

Spawning

Spawning occurs during May or at 0.4 of each year. The fecundity–length function of the yellowtail flounder was assumed to be of the usual form,

$$Fe(L) = c_7 \cdot L^{c_8} \quad (14)$$

where Fe is the egg production of a mature female fish of length L. Not all fish mature at the same age or length. Royce et al. (1959) found that maturation was more closely associated with length than age. A relationship of the following form, expressing the probability of a fish of specific length being mature (P_4) was assumed.

$$P_4 = \begin{cases} y_3 \text{ for } 0 \leq P_3 = c_9 + c_{10}L \leq 1 \\ 0 \text{ for } P_3 < 0 \\ 1 \text{ for } P_3 > 1. \end{cases} \quad (15)$$

Equation (15) assumes maturation is a linear function of length in the transition zone between the length below which the entire population is immature and the length above which the entire population is mature. Assuming that the proportion of females in the population is constant, c_{11}, then the egg production of each age–size compartment is the product of $N_{i,j}$, $Fe(L_{i,j})$, P_4, and c_{11}. The total egg production of the population (P_e) is obtained by summing over all age–size compartments.

Recruitment

The possibilities that recruitment is a linear function of egg production and that recruitment is independent of egg production, under average environmental conditions, were considered. There is evidence (Sissenwine 1974) that recruitment of the Southern New England yellowtail flounder is also related to temperature. In fact, most of the variability in estimated recruitment for 1944–65 was explained by anomalies in air temperature, ignoring egg production. In order to simulate the influence of temperature, a recruitment temperature factor (T_r) was defined as follows:

$$T_r = 1 + c_{12} \cdot (T - \bar{T}). \quad (16)$$

The number of recruitments as affected by temperature is calculated by multiplying the level of recruitment expected at average temperature conditions by T_r.

The total recruitment (R) of a year class (at age 1) is calculated by

$$R = c_{13} \cdot P_e \cdot T_r \quad (17)$$

or

$$R = c_{13} \cdot T_r. \quad (18)$$

The parameter c_{13} has a different value in each equation. Equation (17) is applicable when recruitment is linearly related to P_e for average temperature conditions. Equation (18) is applicable when recruitment is independent of P_e. Equations (17) and (18) will be referred to as the linear and density independent recruitment functions, respectively. The model described in this paper incorporating either Equation (17) or (18) will be referred to as the linear or density independent models, respectively. Recruits are assigned to size categories of age-group 1 by multiplying R by the appropriate value of G_j.

Parameter Estimation

Estimates of the parameters of the model were taken from the literature or based on published or unpublished data sources. The parameter values used in all the simulations reported in this paper (unless otherwise stated) are shown in Table 2 along with citations of the source of the estimate. Special attention is given below to the estimation of some parameters and initial conditions. These estimates of parameters and initial conditions required some subjectivity.

The natural mortality rate of the yellowtail flounder has yet to be precisely estimated. Lux (1969a) estimated that the upper limit on natural mortality of adult yellowtail flounder is 0.20. Beverton and Holt (1957) estimated the natural mortality of a similar species (North Sea plaice) as 0.10. Values of instantaneous natural mortality of 0.10 and 0.20 have been used in the literature in the past. An instantaneous natural mortality rate of 0.10 was assumed for age-groups 3 and older fish in the model. Instantaneous natural mortality rates of 0.4 and 0.2 were applied to age-groups 1 and 2, respectively. Based on a generalized simulation model, Walters (1969) concluded that natural mortality rates, especially in older fish, could vary widely without affecting harvesting strategies.

Brown and Hennemuth (see footnote 2) reported the size-group structure of fish captured and landed by yellowtail flounder fishermen during 1963. According to these data, few fish less than 250 mm long were captured ($L_{g\min}$ = 250 mm). The modal value of Brown and Hennemuth's capture curve is about 330 mm. The modal value usually coincides closely with the length of complete functional recruitment. Therefore, gear efficiency was assumed to reach its maximum at this length ($L_{g\max}$ = 330 mm). All yellowtail flounder less than 300 mm long were discarded at sea ($L_{m\min}$ = 300 mm) and almost all fish captured of greater than 350 mm were landed ($L_{m\max}$ = 350 mm). Of course, market conditions will change with time and there are now reports of some fish less than 300 mm being landed.

TABLE 2.—Value of each parameter used to yield best results with yellowtail flounder model. The parentheses indicate values used for the model in which recruitment is independent of spawning stock. L_{mi} for $i = 1, 2, \ldots, 7$ are given in Table 3.

Parameter	Value	Description	Source
c_1	0.233×10^{-5}	From weight–length function (Equation (4))	Lux (1969b)
c_2	3.233	From weight–length function (Equation (4))	Lux (1969b)
c_3	1.26	First quarter seasonal effort factor	Based on quarterly average effort data for 26 to 50 gross ton vessel reported by Lux (1964)
c_4	0.37	Second quarter seasonal effort factor	Based on quarterly average effort data for 26 to 50 gross ton vessel reported by Lux (1964)
c_5	0.87	Third quarter seasonal effort factor	Based on quarterly average effort data for 26 to 50 gross ton vessel reported by Lux (1964)
c_6	1.49	Fourth quarter seasonal effort factor	Based on quarterly average effort data for 26 to 50 gross ton vessel reported by Lux (1964)
c_7	0.725×10^{-6}	From fecundity–length function (Equation (14))	Pitt (1971) for fish from Grand Bank
c_8	4.69	From fecundity–length function (Equation (14))	Pitt (1971) for fish from Grand Bank
c_9	−1.821	From proportion mature–length function (Equation (15))	Based on percent mature data from Royce et al. (1959)
c_{10}	0.00707	From proportion mature–length function (Equation (15))	Based on percent mature data from Royce et al. (1959)
c_{11}	0.50	Proportion of females	Data on 9,268 fish provided by Northeast Fisheries Center
c_{12}	−0.68 (−0.89)	Slope of recruitment–temperature factor	From recruitment estimates (Sissenwine 1974), see text
c_{13}	5.8×10^{-6} (60.0×10^{6})	Slope of stock–recruitment function	Fitted to catch data with the model, see text
c_{14}	−0.466	Slope of growth–temperature factor	From annual growth estimates (Sissenwine 1975), see text
q	1.68×10^{-4}	Catchability coefficient	Sissenwine (1974)
L_{gmin}	250.0 mm	Minimum size retained by net	From length composition of catch for 1963, see text
L_{gmax}	330.0 mm	Size of maximum net retention	From length composition of catch for 1963, see text
L_{mmin}	300.0 mm	Minimum size at which fish are marketed	From length composition of catch for 1963, see text
L_{mmax}	350.0 mm	Size at which all fish are marketed	From length composition of catch for 1963, see text
$\bar{T}$	10.175°C	Mean temperature	National Weather Service data, Block Island
G_1	0.05	Proportion entering size-class 1	Arbitrary
G_2	0.10	Proportion entering size-class 2	Arbitrary
G_3	0.20	Proportion entering size-class 3	Arbitrary
G_4	0.30	Proportion entering size-class 4	Arbitrary
G_5	0.20	Proportion entering size-class 5	Arbitrary
G_6	0.10	Proportion entering size-class 6	Arbitrary
G_7	0.05	Proportion entering size-class 7	Arbitrary
s_m	33.9 mm	Standard deviation of L_m	Data on 9,268 fish provided by Northeast Fisheries Center
k_1	0.56	Growth rate for fish less than 2 yr	See text
k_2	0.285	Growth rate for fish greater than 2 yr	See text
K_1	0.0	First quarter seasonal growth factor	Based on length by quarter estimates (Lux and Nichy 1969), see text
K_2	0.0	Second quarter seasonal growth factor	Based on length by quarter estimates (Lux and Nichy 1969), see text
K_3	2.0	Third quarter seasonal growth factor	Based on length by quarter estimates (Lux and Nichy 1969), see text
K_4	2.0	Fourth quarter seasonal growth factor	Based on length by quarter estimates (Lux and Nichy 1969), see text
M_1	0.40	Natural mortality of age-group 1	See text
M_2	0.20	Natural mortality of age-group 2	See text
M_i, $i = 3, 10$	0.10	Natural mortality of age-group 3	See text

The annual average air temperature at Block Island was used as an index of temperature on the Southern New England ground because there are no water temperature records of adequate length (1944 to present). Block Island is located on the southwest edge of the Southern New England ground.

Taylor et al. (1957) concluded that air temperature data are a rough index of the general level of surface water temperature. Colton (1968) reported that trends in offshore water masses paralleled trends in surface water temperature at Boothbay Harbor, Maine. Lauzier (1965) used trends in air temperature from 1875 to 1905 as an index of the water temperature of the Gulf of Maine. Templeman (1965) concluded that air temperature at St. John's, Newfoundland, and water temperature at Cape Spear for 1952–62 agreed extremely well.

A record of the bottom water temperature at Lurcher Lightship off Nova Scotia (Lauzier and Hull[6]) was collected from 1951 to 1969. The water depth was about 100 m. The correlation between the average annual bottom water temperature at Lurcher Lightship and the average annual air temperature at Block Island is 0.78. The correlation between the annual average air temperature at Block Island and the annual average surface water temperature at Woods Hole, Mass., for data reported by Chase (1967) is 0.87 during the period 1956–66. The correlation between monthly averages of water temperature at Woods Hole and air temperature at Block Island for this 132-mo time series is 0.98. Therefore, Block Island air temperature record was used as an index of water temperature on the Southern New England ground.

The annual equilibrium catch of a fishery is the level of catch that results in no change in the biomass of the nominal stock (stock suitable for

[6]Lauzier, L. M., and J. H. Hull. 1969. Coastal station data temperature along the Canadian Atlantic coast 1921–1969. Fish. Res. Board Can., Tech. Rep. No. 150, 5 p.

landing). The equilibrium catch is the sum of recruitment and growth (of the individual fish of the nominal stock) minus loss due to natural mortality. Based on this relationship using earlier estimates of equilibrium catch and recruitment (Sissenwine 1974) and assuming annual natural mortality of 0.1, Sissenwine (1975) estimated the average annual weight gain per fish of the Southern New England yellowtail flounder fishery for 1944–65. These estimates ranged from 72 to 331 g/fish per year and are significantly correlated (Kendall rank correlation coefficient (τ) of −0.60) with annual average air temperature at Block Island. Estimates of k of the von Bertalanffy function derived from growth increments of age-classes for 1962–71 were also significantly correlated ($\tau = -0.42$) with temperature at Block Island. Thus, the model was designed to simulate the effect of temperature on growth.

The instantaneous growth rate of a fish is related to k by the following equation:

$$\frac{dw}{dt} = kc_1c_2\,(L_m - L)\,L^{c_2-1}. \qquad (19)$$

Equation (19) was derived by substituting Equation (11) into Equation (4) and differentiating with respect to t. For the values of k, c_1, c_2, and L_m reported by Lux (1969b) and Lux and Nichy (1969), dw/dt is 143, 172, 182, and 163 g/yr for a length of 250, 300, 350, and 400 mm, respectively. Most of the fish in the catch are within this range of length. Therefore, only a minor proportion of the estimated range in annual growth per fish can be accounted for by changes in size composition of the stock. Thus, within the constraints of the model described here (c_1, c_2, L_m do not vary with time), k must be nearly proportional to the rate of weight gain.

During the period 1944–65 there were 4 yr in which the estimated average annual air temperature was greater than 11°C and 7 yr in which it was less than 10°C. For the four warmer years, temperature averaged 11.2°C and growth per fish averaged 88 g. For the seven colder years, temperature averaged 9.5°C and growth 222 g. Assuming k proportional to annual average weight gain per year, c_{14} was estimated as −0.466 by solving:

$$\{1 + c_{14}(11.2 - \bar{T})\}/\{1 + c_{14}(9.5 - \bar{T})\} = 88/222.$$

The proportion of yellowtail flounder recruits entering each size category of age-group 1 was assumed as follows: $G_1 = G_7 = 0.05$, $G_2 = G_6 = 0.10$, $G_3 = G_5 = 0.20$, and $G_4 = 0.30$.

Lux and Nichy (1969) reported a value of 500 mm for parameter L_m of the von Bertalanffy growth function for the yellowtail flounder. They selected this value since it was the maximum length observed. The model described in this paper requires values of L_m for each of the seven size categories. Considering the magnitude of s_m (33.9 mm, see Table 2) a value of 500 mm for L_{m4} may yield fish far in excess of the maximum length observed. Therefore, a more conservative value was used: $L_{m4} = 480$ mm.

The probability density function of L_m was used to calculate values of L_{mi} for $i = 1, 2, 3, 5, 6, 7$. The range of values of L_m represented by each size category (Z_{1i} to Z_{2i}) was calculated based on G_i and the normal density table and found to be as in Table 3. The mean value of L_m for each size category equals the integral of L_m times its density function divided by the integral of the density function (results also shown in Table 3).

TABLE 3.—Range and mean for L_m, the maximum length parameter of the von Bertalanffy growth function, representing each of the size categories of the yellowtail flounder model.

Size category	Range of L_m (mm)	Mean of L_m (mm)	Size category	Range of L_m (mm)	Mean of L_m (mm)
1	0.0–425.1	410.9	5	492.8–514.6	503.0
2	425.1–445.4	436.3	6	514.6–534.9	523.6
3	445.4–467.2	457.0	7	534.9-∞	549.1
4	467.2–492.8	480.0			

Lux and Nichy (1969) estimated the growth rate coefficient (k of the von Bertalanffy growth function) for yellowtail flounder older than 2 yr of age as 0.335. For the period during which Lux and Nichy collected their data, the average annual temperature at Block Island was about 9.8°C. This temperature results in a growth-temperature factor (T_g) of 1.175. Lux and Nichy's estimate was divided by T_g resulting in an estimate of $k_2 = 0.285$. An estimate of k_1 (=0.56) was determined using the model so that fish would grow to a realistic length by age 2.

The seasonal nature of yellowtail flounder growth was exhibited when the average lengths of age-groups were determined quarterly (Lux and Nichy 1969). In general, the mean size of an age-group changes little from the first to the second quarter. Thus, most growth apparently occurs during the second half of the year. In order

to simulate this phenomenon, the following quarterly growth adjustment factors were used: $K_1 = K_2 = 0.0$ and $K_3 = K_4 = 2.0$.

Estimation of c_{12} of the recruitment–temperature factor (T_r, Equation (16)) depends on the form of the recruitment relationship that is assumed. The parameter c_{12} was estimated for both the linear and density independent recruitment functions (Equations (17) and (18)) using estimates of annual recruitment reported by Sissenwine (1974). During 1949–53, recruitment averaged 6.82 million fish (recruits to the stock of marketable fish, about 3 yr and older) with a spawning stock size proportioned to an average relative abundance of 1.4 tons/day and an average annual temperature of 11.08°C. On the other hand, for 1960–63, recruitment averaged 49.7 million fish with a relative abundance and annual average temperature of 2.9 tons/day and 9.65°C, respectively.

For the density independent recruitment function, fluctuations in recruitment result directly from fluctuations in T_g. An increase in recruitment and in T_g by a factor of 7.3 while the temperature anomaly changes from 0.905 to −0.525 provides an estimate of $c_{12} = -0.89$ by solving the following expression:

$$7.3\{1 + c_{12}(0.905)\} = 1 + c_{12}(-0.525).$$

If egg production is assumed proportional to stock size or relative abundance, then for the linear recruitment function, the increase in recruitment by a factor of 7.3 would reflect an increase in spawning stock size by a factor of 2.05 ($\approx$2.9/1.4) and an increase of T_g by a factor of 3.56 ($\approx$7.3/2.05). Therefore, solving the following expression:

$$3.56\{1 + c_{12}(0.905)\} = 1 + c_{12}(-0.525)$$

$c_{12} = -0.68$ for the linear recruitment function.

Since little is known about the survival of yellowtail flounder eggs and their eventual recruitment to age-group 1, c_{13} of the recruitment function was estimated by fitting the model to data (see Verification). The parameter c_{13} was estimated as 5.8×10^{-6} (fish per egg) for the linear recruitment model and as 60.0×10^6 (fish) for the density independent recruitment model.

Both estimates appear realistic as indicated by the following discussion. The average recruitment to the stock of marketable fish reported by Sissenwine (1974) was 22.8×10^6 fish. Assuming an instantaneous natural mortality of 0.4 for age-group 1 and a natural mortality of 0.2 with a total gear mortality of 0.5 ($F + D$) for age-group 2, recruitment to age-group 1 may be crudely estimated by multiplying recruitment to the marketable stock by 3.0. Thus, average annual recruitment to age-group 1 could be estimated as 68.4 $\times 10^6$ fish which is similar to the estimate of c_{13} for the density independent model. For the linear recruitment model, c_{13} is the proportion of eggs that survive to be recruited to age-group 1 under average temperature conditions. Using the average catch per effort for 1943–66 ($U = 2.5 \times 10^6$ g/day), the sex ratio ($c_{11} = 0.5$), the catchability coefficient ($q = 1.68 \times 10^{-4}$), and an estimate of average weight and fecundity (of females) of the nominal stock ($W = 451$ g, $Fe = 700{,}000$ eggs), c_{13} could be crudely estimated as 5.9×10^{-6} using $c_{13} = (R \cdot W \cdot q)/(Uc_{11} \cdot Fe)$. For the winter flounder, *Pseudopleuronectes americanus,* Saila's (1961) work indicated about 18 recruits to age-group 1 per million eggs (actually reported 18 recruits/100,000 hatched eggs assuming 10% hatching success). The value used here is somewhat lower, but the fecundity of the yellowtail flounder is higher than for the winter flounder.

In order to avoid the possibility of recruitment becoming negative for extremely high temperatures, the additional constraint that recruitment never falls below 5 million fish was incorporated into the model.

The initial length and number of individuals of each age–size compartment had to be specified prior to simulating the fishery. Royce et al. (1959) reported the mean length of age-groups 2–6 for the first quarter of 1943. These values were assumed as the initial length of size category 4 of the appropriate age-groups. For the initial lengths of the other age-groups, reasonable but arbitrary values were selected. The average initial size of each age-group is listed in Table 4. The lengths of size categories 1, 2, 3, 5, 6, and 7 were determined by multiplying the length of size category 4 by 0.856, 0.908, 0.950, 1.050, 1.092, and 1.144, respectively. These factors correspond to the ratio of the maximum length of each size category to the maximum length of size category 4.

The onset of the collection of fishing effort data was 1943; therefore, the model was used to simulate the fishery from that date. The relative abundance of the yellowtail flounder during the first quarter of 1943 was 5,742 fish/day (Royce et al.

TABLE 4.—Initial (1 January 1943) mean total length in millimeters of each age-group for yellowtail flounder model. The lengths of age-groups 2–6 were reported by Royce et al. (1959).

Age-group	Mean length (mm)	Age-group	Mean length (mm)
1	160	6	401
2	271	7	425
3	324	8	440
4	353	9	450
5	372	10	460

1959). Dividing this by q, the mean population size during this quarter was estimated as 34.2×10^6 fish. Because there is little growth and, therefore, little recruitment during the first quarter (since fish are recruited as they grow to the size vulnerable to fishing gear), the population was assumed to undergo exponential decay during this time interval. The effort expended during the first quarter of 1943 was 2,038 days (Royce et al. 1959), resulting in a total maturity $Z = 1.47$ ($Z = M + qf$ where f is the rate of fishery in days per year). Accordingly, the size of the landable stock at the beginning of 1943 was estimated as about 41.1×10^6 fish (using Equation 1.38 of Ricker (1975) modified for an interval of one-quarter of a year).

Royce et al. (1959) also reported the age composition for the first quarter of 1943. The catch primarily comprised fish greater than 3 yr of age. The number of fish captured per day for age-group 3 and older is shown in Table 5. Based on the

TABLE 5.—Catch per day and relative abundance adjusted for fishing vulnerability of age-group 3 and older yellowtail flounder for the first quarter of 1943. These age-groups represented 95% of the catch.

Age-group	Catch/day	Adjusted relative abundance
3	1,793	3,984
4	1,596	1,995
5	1,008	1,061
6	504	504
7+	476	476

length composition assumed for each age-group and Equation (9), the relative level of fishing mortality suffered by fish of age 3, 4, 5, and older was calculated as 0.45, 0.80, 0.95, and 1.00, respectively. By dividing the catch per day of each age-group by the appropriate factor, the relative abundance adjusted for fishing vulnerability was obtained (also Table 5). These values represent the relative abundance of each age-group in the population. Using Table 5,

$$N_4 = 0.50\ N_3.$$

$$N_5 = 0.55\ N_4 = 0.280\ N_3.$$
$$N_6 = 0.48\ N_5 = 0.130\ N_3.$$
$$N_7 = 0.50\ N_6 = 0.065\ N_3$$
$$N_8 = 0.50\ N_7 = 0.033\ N_3.$$
$$N_9 = 0.50\ N_8 = 0.016\ N_3.$$
$$N_{10} = 0.50\ N_9 = 0.008\ N_3$$

where the subscript . indicates the summation over all size categories, and the survival of fish older than 7 yr was assumed to be 0.50. The size of the marketable population was estimated by summing N_i times the relative fishing vulnerability of age-group i. This expression was set equal to 41.1×10^6 fish and solved for N_3. ($\approx 32.0 \times 10^6$ fish). Estimates of initial conditions for other age-groups were obtained using the equations in this paragraph. Age-group 2 was assumed to be twice age-group 3 as indicated by a natural mortality of 0.2 and a discard mortality of about 0.5. Based on a natural mortality of 0.40 age-group 1 was assumed to be 1.5 times age-group 2. The initial conditions of each age-group for the beginning of 1943 based on the above discussion are shown in Table 6. The population was distributed among the size categories according to the appropriate values of G_i.

TABLE 6.—Initial size of each age-group of yellowtail flounder population assumed at the beginning of 1943.

Age-group	Number in thousands	Age-group	Number in thousands
1	95,000	6	4,200
2	64,000	7	2,100
3	32,000	8	1,100
4	16,000	9	530
5	8,800	10	260

VERIFICATION

The primary mode of verification of the model was to compare predicted annual levels of catch with published values. Lux's (1969a) record of catch and fishing effort for 1943–66 is in conflict for several years with data reported by Brown and Hennemuth (see footnote 2) in an unpublished form. These conflicts are minor, except for the 1966 catch where the difference is about 40%. Since this year is at the end of the published record and could easily be ignored, 1943–65 were initially used for verification. After c_{13} was fit to the data, the model was then compared with data through 1972.

Before comparing the model with the published data, it was necessary to select a time step or

integration interval that would not result in unreasonable numerical errors being propagated through many years of simulated time. This was done by increasing the time step until the simulation results converged. With an integration interval of 0.005 yr, the results converged sufficiently so that a numerical error of less than 5% is expected after 23 yr of simulation (the length of the data record used for verification). This level of error was considered acceptable in light of the precision of all the data upon which this work was based. It was noted that each decrease in the time step was accompanied by an increase in the simulated catch; therefore, the predictions yielded by the computer simulations are probably slightly lower than would have resulted from an exact solution of the model.

The average length of age-groups 2–5 according to the model for 1943–66, 1957–62, and 1962–71, and the average length of these age-groups as reported by Lux and Nichy (1969), and of the catch for 1962–71 are compared in Table 7. Age-groups 2–5 were considered because they were most abundant in available samples; and, therefore, their means have smaller standard errors than less abundant age-groups.

Most of the fish measured by Lux and Nichy were collected during 1957–62. Model results for this period compare favorably as expected since the model was designed to simulate the situation reported by Lux and Nichy. The average simulated lengths for 1943–66 are generally lower than for the 1957–62 design period since the design period had a lower temperature (favorable to growth) than the longer time interval.

The model tends to overestimate growth for 1962–71. The mean length of fish of a particular age-group collected from the catch for 1962–71 is lower than is predicted by Lux and Nichy's growth function. This situation cannot be explained as an effect of temperature. As has been the practice throughout this work, the model was designed in accordance with the published literature; therefore, some apparent overestimation of growth in later years of the simulations is inevitable. This situation makes application of the model less satisfactory for recent years, but part of the effect of overestimating growth would be compensated for by a shift in age-group structure of the catch. If the model slightly overestimates growth, there is a tendency to catch younger fish; and, therefore, the effect of overestimating growth is partially offset.

The simulated size-category structure of captured (landed and discarded) fish for 1943–65 is compared with unpublished data for 1963 as reported by Brown and Hennemuth (see footnote 2) in Figures 2 and 3. Clearly, it would have been

TABLE 7.—Average length (millimeters) of yellowtail flounder age-groups 2–5 according to the model for 1943–66, 1957–62, and 1962–71 according to Lux and Nichy (1969), and for samples from the commercial catch collected January–March 1962–71 (data provided by Northeast Fisheries Center).

Age-group	Model 1943–66	Model 1957–62	Model 1962–71	Catch samples 1962–71	Lux and Nichy
2	275	290	323	306	266
3	303	338	365	342	338
4	351	367	397	365	378
5	378	385	416	387	404

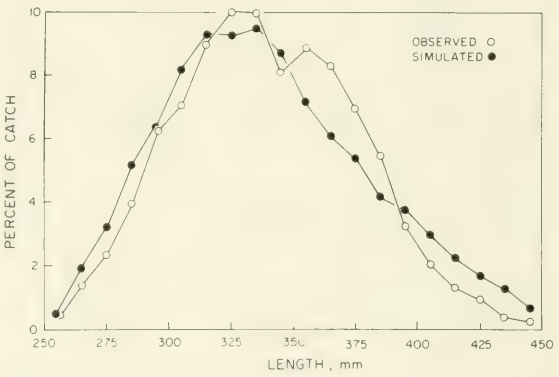

FIGURE 2.—Simulated (1943–65) and observed (unpublished data for 1963 as reported by Brown and Hennemuth (see footnote 2)) size-category structure of catch (including discards) of yellowtail flounder.

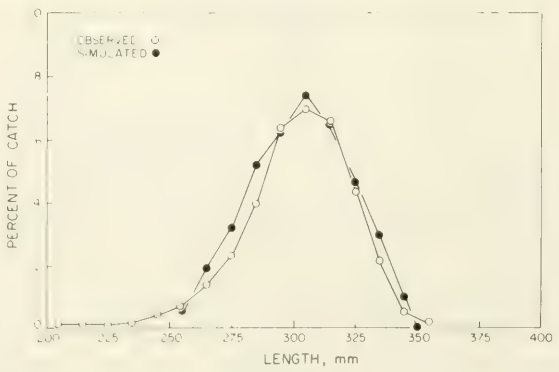

FIGURE 3.—Simulated (1943–65) and observed (unpublished data for 1963 as reported by Brown and Hennemuth (see footnote 2)) size-category structure of discards as percentage of catch (including discards) for yellowtail flounder.

better to compare the 1963 simulated size-category structure with these data, but, because of a programming oversight, this information was not available. The comparisons in Figures 2 and 3 are generally favorable and indicate that the assumed linear relationships (Equations (6) and (7)) describing the relative effectiveness of the fishing gear and the marketability of fish as a function of length were adequate. The model indicates that 39.5% of the fish captured by fishermen for 1943–65 were discarded. The average weights of landed and discarded fish based on Figures 2 and 3 are 455 and 249 g, respectively.

The parameter c_{13} of the recruitment function (Equations (17) and (18)) was estimated by running the model for several values of this parameter and selecting the value that explained the greatest proportion of variation in observed yield. Of the values considered, c_{13} equal to 60.0×10^6 and 5.8×10^{-6} for the density independent and linear recruitment models were most successful in explaining variation in yield. Since only a finite number of values of c_{13} were considered, the values selected are probably not the "best least squares" estimates, but the results (Table 8) indicate that the model is not very sensitive to 5–10% fluctuations in this parameter. As noted earlier, these values appear realistic.

TABLE 8.—Percent of variation in yield explained by the yellowtail flounder model with various values of c_{13} for 1943–65.

c_{13}	Linear stock-recruitment (%)	c_{13}	Density independent stock-recruitment (%)
5.4×10^{-6}	73.6	55.0×10^6	81.3
5.6×10^{6}	82.0	57.5×10^6	82.6
5.7×10^{6}	84.5	60.0×10^6	83.2
5.8×10^{6}	85.5	$62.5 \cdot 10^6$	83.0
6.0×10^{6}	82.3	65.0×10^6	82.1
		70.0×10^6	78.1

The model using linear or density independent recruitment explained 85.5 and 83.2% of the variation in yield from 1943–65, respectively. In addition to catch and effort data reported by Lux (1969a), catch data through 1972 and effort data through 1971 were available (at the time when this research was in progress) for the Southern New England ground (Brown and Hennemuth see footnote 2; Brown see footnote 3; and Parrack see footnote 4). Both the linear and density independent stock-recruitment models were run for 1943–72 (assuming that the level of effort was unchanged from 1971 to 1972), and the results were compared with the available data in Figures 4 and 5. Both models seem to simulate catch as well since 1965 (although yield is substantially underestimated for 1969 and 1970) in spite of the fact that they were developed independently of the later data and that growth is apparently somewhat overestimated toward the end of the simulation. Since errors for any particular

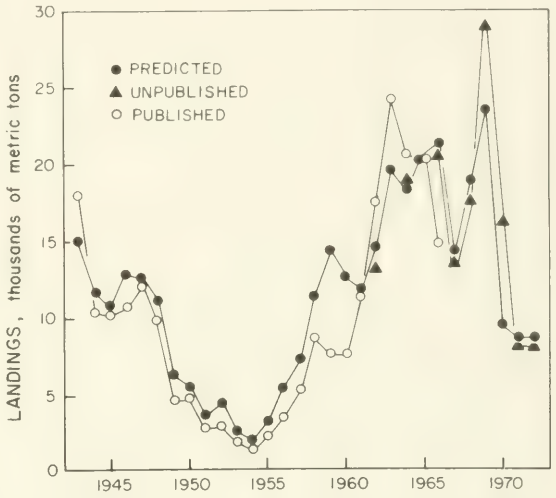

FIGURE 4.—Landings of Southern New England yellowtail flounder as reported in published and unpublished reports and predicted by the model with linear recruitment function (Equation (17)).

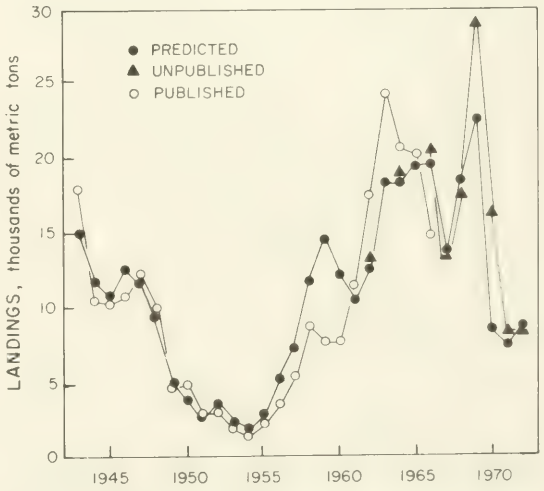

FIGURE 5.—Landings of Southern New England yellowtail flounder as reported in published and unpublished reports and predicted by the model with a density independent recruitment function (Equation (18)).

year are propagated through the simulation, it is surprising that the model seems to recover after occasional substantial deviations from the observed yield.

Sissenwine (1974) explained most of the variability in recruitment of the Southern New England ground even though the size of the spawning stock was ignored. This earlier work noted that spawning stock size may have an important effect on recruitment, but the effect might be obscured by environmental noise. The work reported here demonstrates that models incorporating either linear or density independent recruitment explain most past variability in catch of the fishery. Nevertheless, the model incorporating recruitment linearly dependent on spawning stock size is preferable for the following reasons:

1. While the linear model only explained 2.2% more variation than the density independent model, it did explain 13% of the density independent model's residual variation with no increase in number of parameters.
2. While the density independent model is more simplistic mathematically, a direct linear relationship between stock size and recruitment is a more basic biological relationship. Obviously, recruitment cannot be independent of spawning stock size over its entire range. The density independent situation can only exist as a special case of a more complex nonlinear stock-recruitment relationship.
3. It seems unrealistic for recruitment to be unaffected by size of spawning stock when stock size varies by a factor of 3.
4. The linear stock-recruitment model is a more conservative management tool than the density independent model. Management practices designed to prevent a dangerous reduction in stock size of a population regulated by a linear stock-recruitment relationship will also prevent a reduction in stock size of a population regulated by a density dependent stock-recruitment relationship.

No attempt was made to use the Ricker (1954, 1958) stock-recruitment function or other nonlinear functions because the results obtained using the linear and density independent functions (Equations (17) and (18)) indicated that most likely these more complicated functions would not significantly increase the accuracy of the model. When using the linear model where the Ricker function (for example) is more appropriate, the linear model is expected to be accurate at low population levels but overestimates recruitment (and catch) at higher population levels. The reverse situation is expected when the density independent model is used where a Ricker function is more appropriate. In neither case was the more complex Ricker function indicated.

Based on the above discussion, the linear stock-recruitment function (Equation (17)) seemed most appropriate over the observed range of population size. Therefore, only the linear model is used in the remainder of this paper.

The linear stock-recruitment model was run for 1943–65 without temperature dependent growth ($c_{14} = 0.0$), without temperature dependent recruitment ($c_{12} = 0.0$), and without temperature dependent growth or recruitment ($c_{12} = c_{14} = 0.0$). None of these situations explained a significant portion of variation in catch. This fact does not constitute rigorous evidence that incorporation of T_g and T_r into the model is necessary to explain most of the variability in catch because no attempt was made to tune the model for the temperature independent cases. Earlier work by Sissenwine (1974, 1975) demonstrated the influence of temperature on the fishery and supports the incorporation of T_g and T_r into the model.

APPLICATIONS

The effects of several alternative fishing strategies were examined using the model. These examples deal with some aspects of the model which are not common components of other fishery models (such as discard mortality, temperature dependence, and seasonal growth and fishing rate).

The impact of discarding at sea fish shorter than 300 mm was evaluated by running the model with the assumption that the minimum size retained by a net equaled this value. The results for $L_{g\min} = 300$ mm are compared with the model results as described earlier ($L_{g\min} = 250$ mm) in Figure 6. Landings in excess of 30,000 metric tons are not shown because these have not been observed during the history of the fishery; thus simulations indicating these high values are extrapolative in nature. These higher simulated landings result because the model assumes a linear stock-recruitment relationship at all stock sizes, while in reality the relationship probably becomes density dependent as stock size becomes large. By eliminating discard mortality of fish shorter

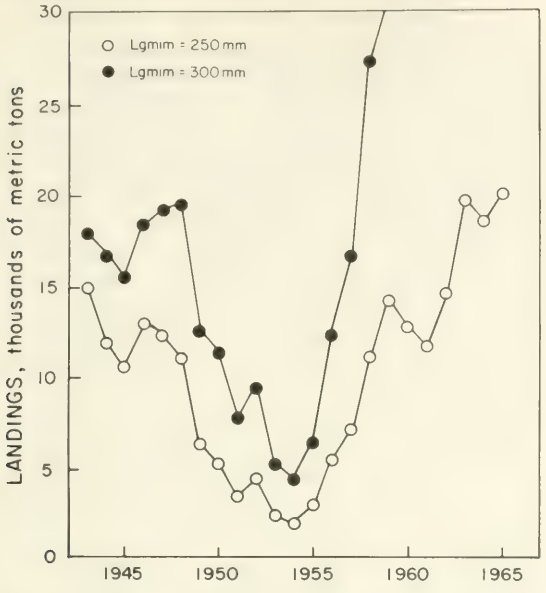

FIGURE 6.—Simulated landings of yellowtail flounder with L_{gmin} = 250 mm and 300 mm. Landings greater than 30,000 metric tons are not shown.

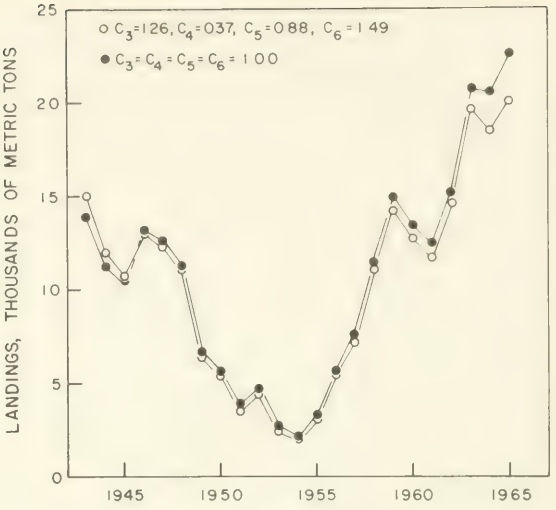

FIGURE 7.—Simulated landings of yellowtail flounder with fishing effort applied uniformly and with c_3–c_6 as assumed for 1943–65.

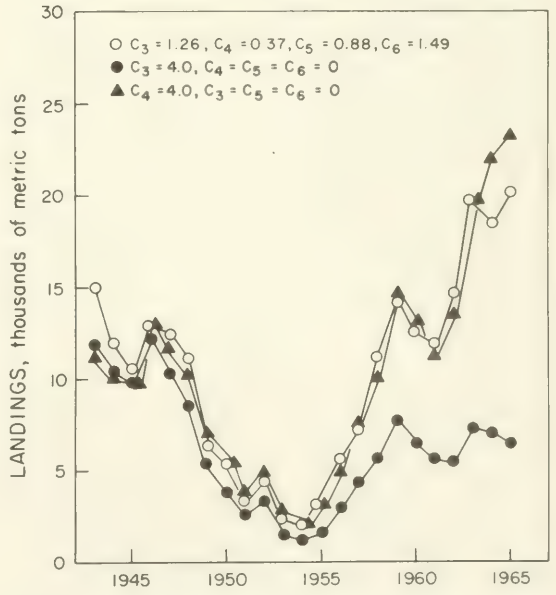

FIGURE 8.—Simulated landings of yellowtail flounder with all fishing effort in the first or second quarter of the year and with c_3–c_6 as assumed to have occurred for 1943–65.

than 300 mm, these fish have a higher probability of surviving until they are recruited and spawn. The result was from a 20% to a severalfold increase in landings.

Using the Beverton and Holt yield per recruit (YPR) function, Brown and Hennemuth (see footnote 2) found less than a 40% increase in yield by delaying the age at first capture from 1.75 yr (or 245 mm) to 2.5 yr (or 302 mm) for F less than 1.1. This was the highest simulated fishing mortality rate during 1943–65. The substantially greater increase in yield from the simulation reported in Figure 6 results from increased recruitment which is not considered in the Beverton and Holt YPR function.

The benefit of increasing mesh size to eliminate discard mortality is clearly demonstrated (for the linear recruitment model), but this analysis ignores financial and technological difficulties which may be involved (Gates and Norton 1974).

The effect of the seasonality of fishing mortality was explored by varying seasonal effort adjustment factors (c_3, c_4, c_5, and c_6). Situations where effort was applied uniformly throughout the year and where all effort was applied during a single quarter were considered. These cases are compared with the results reported earlier (c_3 = 1.26, c_4 = 0.37, c_5 = 0.88, and c_6 = 1.49) in Figures 7–9 and Table 9.

The simulations reported in Figures 7–9 indicated that the seasonal aspect of the expenditure of effort and resulting fishing mortality could

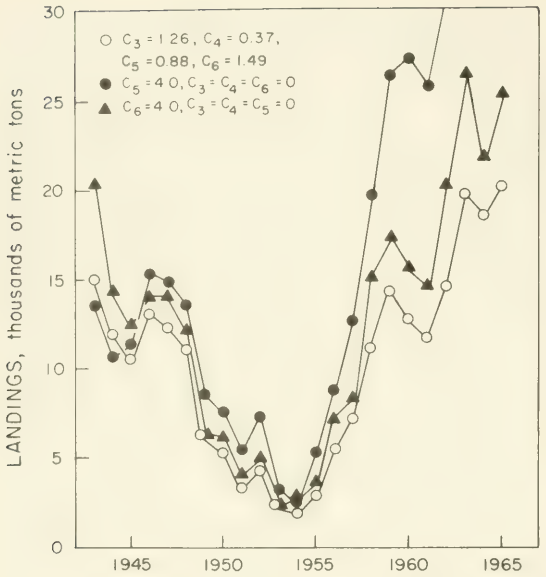

FIGURE 9.—Simulated landings of yellowtail flounder with all fishing effort in the third or fourth quarter of the year and with c_3–c_6 as assumed to have occurred for 1943–65.

TABLE 9.—Comparison of simulated catches of yellowtail flounder with various values of the seasonal effort factors (c_3, c_4, c_5, c_6). Percentage changes in yield are relative to the simulated yield with c_3, c_4, c_5, and c_6 as in the first line of the table.

				Percentage change in yield		
c_3	c_4	c_5	c_6	1943	1944	1943–65
1.26	0.37	0.88	1.49	—	—	—
1.00	1.00	1.00	1.00	−6.7	−4.5	+3.6
4.00	0.0	0.0	0.0	−20.7	−14.3	−40.6
0.0	4.00	0.0	0.0	−24.0	−16.8	−0.6
0.0	0.0	4.0	0.0	−9.4	−9.3	+92.8
0.0	0.0	0.0	4.0	+36.4	+21.0	+22.6

have a very significant impact on the yield of the fishery. There was little change in yield indicated when fishing mortality was assumed uniform throughout the year. The simulations showed that yield of the simulated fishery would have been reduced if all fishing mortality occurred during the first quarter of the year. If all fishing mortality were applied during the second quarter, yield of the fishery would have been lower during the first few years of the simulation, but little difference in total yield is indicated over 23 yr. The expenditure of effort during the third quarter also tended to reduce the early catch, but in the long run appeared to result in the highest yield. By restricting fishing mortality to the fourth quarter of the year, some initial increase in catch was indicated and long-term yield was also increased.

These results reflect the facts that spawning occurs during the second quarter and growth of fish is limited to the third and fourth quarters of the year according to the model. Clearly, to obtain a short-term gain in yield, it is most advantageous to harvest at or near the end of the growing season (Table 9). Long-term gains were obtained when egg production was optimized by harvesting just after spawning (third quarter). By concentrating effort during the fourth quarter, an increase in yield was indicated for all years of the simulation. Fishing during the first quarter appears to be particularly detrimental because it crops fish just prior to spawning.

The seasonal pattern of effort exhibited by the fishery in the past includes intense fishing during the first quarter and the fourth quarter of the year. Apparently these balance, resulting in yields similar to the case where fishing is uniform through the year. In recent years, the annual catch quota for the United States (established by the International Commission for the Northwest Atlantic Fisheries (ICNAF)) was divided equally among the four quarters. The result is that fishing mortality was probably distributed nearly uniformly through the year. There may be some advantage to increasing the portion of the annual quota captured during the second half of the year. It is important to note that the long-term gains obtained by concentrating fishing just after the spawning season will not be realized if recruitment is independent of spawning stock size (Equation (18)).

Several experiments were conducted with the model in order to determine to what degree the yield of the fishery could be stabilized or increased by regulating the annual expenditure of effort and ultimately F. For a fishery in which recruitment is linearly related to stock size, in the long run it is advantageous to reduce fishing effort (and mortality) in order to increase egg production. Therefore, the fishery was simulated with effort at 80% of observed values (Figure 10). The short-term decrease in yield was rather minor. Considerable long-term advantage was predicted; but even with a reduced level of effort, the simulated fishery declined during the late 1940's and early 1950's. However, the recovery when conditions became favorable was more rapid at the lower level of effort for this particular case.

The Beverton and Holt YPR equation (Brown and Hennemuth see footnote 2) indicates less than a 5% increase in catch with a 20% decrease in

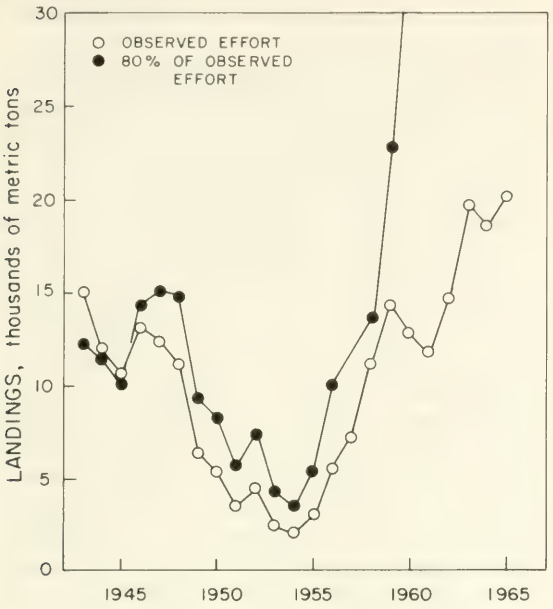

FIGURE 10.—Simulated landings of yellowtail flounder with observed level of fishing effort and with 80% of the observed level.

fishing mortality (for $0.6 \leq F \leq 1.5$ and age at first capture between 1.75 and 3.0). Therefore, most of the increase in yield indicated in Figure 10 must result from improved recruitment at lower levels of F.

Since recruitment and growth appear related to temperature, the possibility of using this environmental variable to predict an appropriate level of effort was considered. The model is such that growth and recruitment are proportional to T_g and T_r, respectively. Therefore, the following relationship between fishing effort and T_g and T_r was utilized:

$$f_i = c_{15} \cdot \{(T_g)_{i-1} + (T_r)_{i-2}\}. \qquad (20)$$

Effort for year i was based on the growth–temperature factor for the year $i - 1$ since Equation (20) is of little value unless effort can be set in advance. The recruitment–temperature factor from 2 yr prior ($i - 2$) was used since recruitment lags spawning by about 2 yr. A 3-yr lag could have been used. T_g and T_r could have been weighted in Equation (20) since the latter is usually more important in determining equilibrium yield, but this would have introduced another parameter.

Initially, c_{15} was estimated as 1,870 days of fishing, which yields about the average level of effort for 1943–65 when T_g and T_r equal 1. A value higher and lower than 1,870 days was also considered. Simulated catches for each value of c_{15} are shown in Figures 11–12, and the simulated catch per unit of effort is shown in Figure 13.

For 1943–65, c_{15} = 2,200 days resulted in a decrease in relative abundance while c_{15} = 1,540 days permitted the relative abundance to increase. The value of c_{15} (1,870 days) corresponding to the average effort during 1943–65 best stabilized the relative abundance of the fishery, but was only slightly more effective than the voluntary actions of the fishermen who probably responded to fluctuations in fishing success (U). It appears that a function even more sensitive to temperature than Equation (20) is required to better stabilize the population. Since T_r is more sensitive to temperature than T_g, weighting of these factors (in favor of the former) might result in a function more effective in maintaining the population size during the early 1950's. Nevertheless, the yield of the simulated fishery (with the linear recruitment function) could have been substantially increased if fishing effort were regulated by a simple function such as Equation (20) with c_{15} considerably less than 1,870 days.

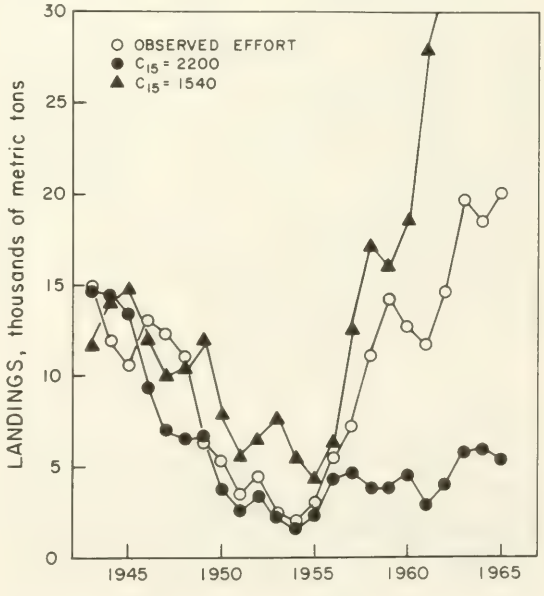

FIGURE 11.—Simulated landings of yellowtail flounder with observed effort and with effort set by Equation (20) using c_{15} = 2,200 or 1,540.

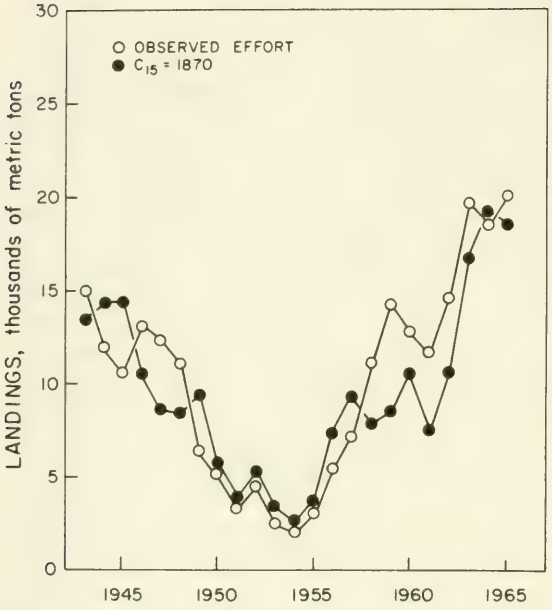

FIGURE 12.—Simulated landings of yellowtail flounder with observed effort and with effort by Equation (20) using c_{15} = 1,870.

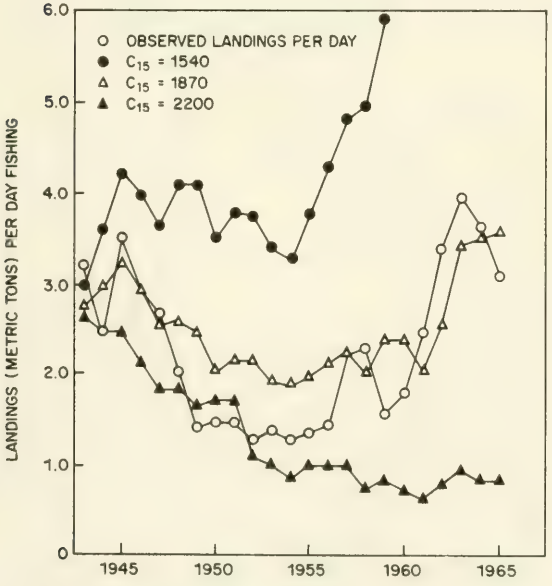

FIGURE 13.—Observed catch of yellowtail flounder per day of fishing and simulated catch per day with effort set by Equation (20) using c_{15} = 1,540, 1,870, or 2,200.

At present, annual catch quotas for the Southern New England yellowtail flounder stock are based on a prerecruit index (Brown and Hennemuth 1971). The index is calculated from the catch of 1-yr-old fish in an autumn bottom trawl survey (Grosslein 1969). Thus the major source of variability in production resulting from the influence of temperature on recruitment is accounted for in current stock assessments. This model should not be considered as an alternate method of management of the fishery on a year to year basis without further verification and refinement.

Walters (1969) developed a yield optimization procedure for his generalized fish simulator using the steepest ascent method. The development of an optimization procedure for the model reported in this paper would be more difficult because this model is driven by two exogenous factors, temperature and the rate of fishing, while Walters's model is only driven by fishing mortality. This model is generally more complex than Walters's model and much more expensive to run. Therefore, the development of an optimization procedure is beyond the scope of the present work.

DISCUSSION

A complex compartmentalized simulation model of the Southern New England yellowtail flounder fishery has been described, verified against catch statistics, and used to examine methods of increasing yield. The relationships and parameters upon which the model was based do not appear to be unreasonable since most variability was explained. Nevertheless, in retrospect, some consideration of alternate approaches to estimating parameters and of modifications of the model is appropriate. It is important to remember that there may be numerous other models or parameter values equally as successful at explaining variation in catch as the one proposed here.

An average maximum length (L_{m4}) for the simulated population of 480 mm was assumed. This value was used in order to assure that few fish would exceed 500 mm in length. When fishing pressure was applied to the simulated population, its average maximum length was suppressed. For some years, the average length of the older agegroups converged to about 460 mm. Since the growth rate coefficients (k_i) of adult fish were based on Lux and Nichy's (1969) work where a maximum length of 500 mm was assumed, the model tends to underestimate the length of older fish. In order to compensate for this effect, the growth rate coefficient of fish younger than 2 yr of age was overestimated. The result was that

the mean size of younger fish was higher than observed while the converse applied to older fish. The differences were generally small. The sizes of the most abundant fish in the catch (age-groups 3 and 4) were well simulated. While the model adequately simulates growth, more precise results might have been obtained by assuming an average maximum size in excess of 500 mm. The result, with fishing, would be an average maximum size near the value assumed by Lux and Nichy (1969). Thus the assumed value of k_2 would have been more appropriate.

The parameters of c_{12} and c_{14} specify the temperature dependence of the model. Estimates of these parameters were based on Sissenwine's (1974, 1975) calculations of recruitment and average growth per fish for 1944–65. No attempt was made to improve these estimates by tuning them to the model. While Figures 4 and 5 indicate the adequacy of the model and its parameters, these figures also reveal that catch was generally overestimated during warm years and underestimated during cold years. This implies that the fishery was probably more sensitive to temperature than indicated by estimates of c_{12} and c_{14}. Rather minor adjustment of these parameters would probably account for much of the remaining unexplained variation in catch. On the other hand, since tuning in effect reduces the residual degree of freedom and, more subjectively, reduces confidence in the model, no attempt was made to improve the initial estimates of c_{12} and c_{14}.

Adult female yellowtail flounder are generally longer than males of the same age. The model does not distinguish between sexes. To do so would require doubling the central processing time required to run the model. Fishing pressure would tend to shift the sex ratio in favor of males because of this size difference. Since the sex ratio ($c_{11} = 0.5$) was estimated for the exploited population, the influence of fishing was incorporated into the model through the estimation of this parameter. Variations in c_{11} resulting from changes in level of fishing were not simulated.

Since females are larger than males, the total fecundity of the population is underestimated when based on the mean size of the age–size compartments. This bias is probably compensated for by overestimating mean recruitment per egg (c_{13}). Thus, expansion of the model to segregate fish according to sex should not affect the results reported here, although some revision of c_{13} would be required.

In recent years, several changes have occurred in the Southern New England yellowtail flounder fishery that were not reflected in the model. During the late 1960's, more active industrial and distant water fisheries (using small mesh nets) for the yellowtail flounder developed. The fisheries statistics used in this report do not include the catch of the industrial fishery which in a few years equaled 20% of the total yield. Estimates of the catch of the distant water fishery are included and the fishing effort of the distant water fleet is estimated by assuming that the catch per unit effort was the same as for the domestic fishery. Since 1971, the fishery has been regulated by quotas set by ICNAF. During the 1970's, landings of yellowtail flounder within ICNAF Subarea 6 (south of the Southern New England ground which is within ICNAF Subarea 5) have increased. The relationship between the fisheries in these two areas is unknown (Brown see footnote 3; Parrack see footnote 4). These recent changes necessitate several modifications of the model before it can be used to simulate the present fishery.

The work reported here indicates the potential for predicting future trends of certain well-studied fisheries in which the role of a specific environmental variation can be described. Two important limitations of this approach are demonstrated. Firstly, model parameters may change with time; thus it is important to keep the model up-to-date. This does not imply that the model should be regularly tuned to assure that it successfully predicts each additional year of data but rather that parameters be updated as evidence of change in the fishery becomes available. Secondly, numerous fundamentally different models may be nearly as successful in simulating a specific system. Therefore, it is dangerous to limit consideration to a single model or regulatory mechanism.

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INCOME ESTIMATES AND REASONABLE RETURNS IN ALASKA'S SALMON FISHERIES[1]

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ABSTRACT

Earnings in some fisheries may fall to a level that is unacceptable from the viewpoint of public policy. Using the Alaska salmon fisheries as an example, this paper examines a method for establishing the number of operating units that will provide a reasonable economic return in a fishery. Estimates are provided of the rates of return that can be expected with various numbers of operating units. Three criteria are then developed to determine a reasonable rate of return. These criteria include: 1) a comparison with wages in a similar industry in an equal time period, 2) a comparison with total annual incomes from all sources with total incomes of workers in other occupations, and 3) an estimate provided by fishermen themselves. These three different measures indicate an optimum number of operating units within a fairly narrow range. In some fisheries it appears that substantial reductions in the number of fishing units will not be sufficient to raise incomes to an "acceptable" level. This raises questions about the allocation of valuable fishery resources among various user groups.

During the last two decades economists have developed a general theory of a common property fishery under conditions of open access. The salient implications of that theory are that: 1) there is a danger that the resource will be fished beyond maximum sustained yield, 2) the resource will not be harvested with maximum economic efficiency, and 3) there will be a misallocation of productive factors between the fishing sector and other sectors of the economy (Crutchfield and Pontecorvo 1969). Empirical research has shown that there may be a fourth consequence of open access that is not adequately dealt with in the theoretical literature. This is the fact that earnings of fishermen under conditions of open access may fall below a level that is acceptable from the viewpoint of public policy (Sinclair 1960; Owers 1974; Huq[3]; Smith[4]). The public interest arises from the fact that poor earnings have been responsible for creating sanitation, health, safety, and other hazards; that programs providing government assistance for fishermen are becoming increasingly expensive; and that in many cases commercial users can no longer afford to pay their share of management costs. The cause of the problem appears to be the very low opportunity costs of fishermen who have only an avocational interest in fishing or else have little mobility and limited access to alternative employment.

Data collected by interview and from landing records indicate that 44% of the purse seiners, 15% of the drift gill netters, and 60% of the set gill netters in Alaska showed a net loss in 1973 (Smith et al.[5]). In the same year, the average net return to the more than 6,400 gear operators who participated in those salmon fisheries which now have limited entry was about $1,600 per gear operator.

Recognition of the recurring problems created by low earnings in many of the state's fisheries led Alaska to pass the first comprehensive limited entry law in the United States in 1973. The law directs an independent commission to stabilize or reduce the number of legal units of gear that can be fished in those fisheries where economic or biological conditions require it. Specifically the law states the following must be considered in establishing an economically sound number of entry permits: "The number of entry permits sufficient to maintain an economically healthy fishery that will result in a reasonable average

[1]The opinions and conclusions set forth in this paper are not those of the Commercial Fisheries Entry Commission nor the State of Alaska.

[2]Cornell Law School, Myron Taylor Hall, Ithaca, NY 14853.

[3]Huq, A. M. 1971. A study of the economic impact of changes in the harvesting labor force in the Maine lobster fishery. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., contract 14-17-007-1121, Wash., D.C., 34 p.

[4]Smith, F. S. 1974. 1972 commercial fishermen survey. Dep. Agric. Econ., Oreg. State Univ., Corvallis, 7 p.

[5]Smith, F. S., D. Liao, J. Martin, and P. Adelman. 1975. Profitability analysis for Alaska fishing businesses. Dep. Agric. Econ. Oreg. State Univ., Corvallis, 13 p.

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rate of economic return to the fisherman participating in that fishery considering time fished and necessary investments in vessels and gear . . . (Anonymous 1973a)." As used in the law and this discussion, a "fishery" refers to a specific combination of species, gear type, and management district. Figure 1 shows the salmon management districts in the state. An entry permit entitles the holder to operate a legal unit of gear in a fishery.

In 1974 entry was limited in the power troll fishery and all salmon net fisheries, with the exception of those in the Arctic, Yukon, and Kuskokwim management districts. This paper examines a procedure that can be used to evaluate the gear cutbacks that may be required to achieve "reasonable" earnings in these fisheries. Because the limited entry law seeks to achieve a balance among social objectives, biological management, and economics, the reductions suggested here, which consider only possible economic objectives, are not necessarily those which the law would require.

A detailed discussion of sample size, methodology, and other factors affecting the validity of data used can be obtained from several of the references cited at the end of the article. Further elaboration is not provided in the text, other than to briefly describe the data used and its source. It should be further recognized that it is not the purpose of this paper to present a rigorous mathematical definition of a problem, but rather to point out its general magnitude and direction.

ESTIMATING EXPECTED RETURNS IN THE SALMON FISHERIES

Several equations were used to estimate returns salmon fishermen might receive with various numbers of operating units in the fisheries. All the equations are presented below, followed by a more detailed description of the variables. Table 1 summarizes the input data used in the equations. To estimate gross returns per operating unit in each fishery, the following equation was used:

$$G = \frac{T \cdot (1 + S)}{P \cdot E} \tag{1}$$

where G is the gross return per fishing unit in the particular fishery; T is the total exvessel revenue paid to all fishermen in that particular fishery; S is the percent of revenue paid as bonus payments to fishermen; P is the percent of entry permits actually used in a particular fishery; and E is the total number of entry permits outstanding.

To estimate net returns per entry permit holder, exclusive of opportunity costs of capital, the following equation was used:

$$N_1 = G - \frac{T \cdot L}{P \cdot E} - C \tag{2}$$

where N_1 is net return not including the opportunity cost of capital; L is the percent of total

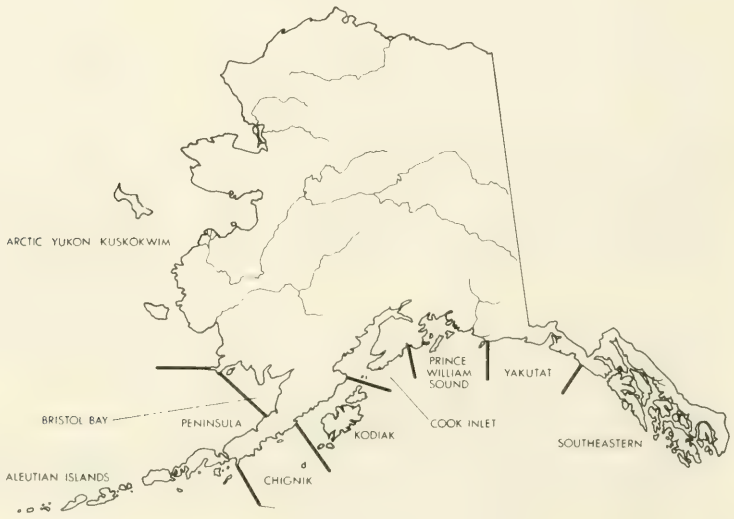

FIGURE 1.—Alaska salmon management areas.

TABLE 1.—Input data used to generate estimates of fishermen's incomes by fishery.

Fishery	Total exvessel revenue (T) in thousands[1]	Costs (C) per operating unit[2]	Crew share (L) [fraction of T paid][2]	Net earnings from other fisheries (X)[2]	Market value of investment (I)[2]	Fraction of gross return earned in other fisheries (F)[2]	Estimated fraction of permits actually (P) fished[3]	Earnings from nonfishing sources (O)[4]	Bonus payments (S) [fraction of T][2]	No. of entry permits issued (E)
Purse seine:										
Southeast	$9,750	$10,279	0.500	$7,390	$91,212	0.46	0.87	$4,155	0.196	395
Prince Wm Sound	4,385	5,804	.450	2,128	39,592	.31	.89	3,016	—	238
Cook Inlet	467	4,506	.510	2,607	33,657	.37	.61	4,343	.004	68
Kodiak	5,947	4,805	.430	—	37,902	.33	.91	4,685	.019	368
Chignik	2,541	10,213	.420	—	66,307	.18	.95	2,007	.045	80
Peninsula-Aleutians	1,603	1,627	.340	8,703	51,473	.74	.78	4,061	—	111
Drift gill net:										
Southeast	4,404	4,381	.072	2,583	27,254	.12	.74	4,012	.092	453
Prince Wm Sound	3,063	4,436	.058	879	15,642	.23	.79	1,906	.024	511
Cook Inlet	2,235	2,744	.176	589	15,254	.17	.67	2,501	.029	545
Peninsula-Aleutians	1,526	3,780	.092	1,171	23,428	.22	.83	1,925	—	155
Bristol Bay	13,933	1,879	.380	—	11,548	.12	.85	3,378	—	1,669
Set gill net:										
Yakutat	476	[5]2,930	—	—	[5]8,223	—	.82	1,632	—	150
Prince Wm Sound	119	[5]2,930	—	—	[5]8,223	—	.68	3,540	—	32
Cook Inlet	1,508	2,930	—	—	8,223	—	.71	3,874	.002	686
Kodiak	459	2,590	—	—	8,139	—	.83	1,511	.050	183
Peninsula-Aleutians	226	1,485	—	—	4,317	—	.48	318	—	77
Bristol Bay	1,248	1,021	—	—	1,758	—	.78	473	—	803
Power troll:										
Statewide	5,290	3,580	.272	2	33,002	.36	.88	3,439	.026	895

[1]Computed from landing records of the Alaska Department of Fish and Game for the years 1969–73. Adjusted by Wholesale Price Index using 1973 as a base year.
[2]Information gathered from a cost survey of Alaskan fishermen (Source: Owers 1974).
[3]Computed from landing records and license files of the Alaska Department of Fish and Game for the years 1969–72.
[4]Information gathered from a random sample of gear license holders. Reported from Internal Revenue Service in confidential format that did not reveal individual identities.
[5]No reliable data. Data from Cook Inlet used as an approximation.

exvessel revenue paid to crewmembers, exclusive of the entry permit holder; and C is expenses per vessel.

To estimate net returns to the entry permit holder, including the opportunity cost of capital, the following equation was used:

$$N_2 = N_1 - A \cdot B \cdot I \cdot (1 - F) - 2 \cdot N_1 \cdot B \quad (3)$$

where N_2 is the net return less opportunity capital costs; A is a constant term used to deflate the average value of investment; B is a constant used for the opportunity cost of capital; I is the average total value of investment per operating unit in the fishery as estimated by fishermen; and F is the percent of income received in other fisheries.

Finally, to estimate the entry permit holder's total annual income from all sources, the following equation was used:

$$Y = N_1 + X + O \quad (4)$$

where Y is total annual income; X is net earnings from other fisheries; and O is income earned from employment other than commercial fishing.

All these equations provide an estimate of the average rate of return per entry permit holder or operating unit in a particular fishery. Analysis of fish landings indicates that a large number of fishermen participate only a short period out of the total fishing time available. A study of returns in Alaska's fisheries shows there is evidence that the time an operator spends fishing is correlated with profit (Smith et al. see footnote 5). Therefore, the average rate of return discussed here is assumed to be the potential earnings of a fisherman who participates during the entire season in that particular fishery but, it is still likely that there will be some concentration of landings by top producers.

A further simplifying assumption in these equations is that the resource will be harvested at the same level of output with all the various numbers of operating units considered. Preliminary estimates provided by management biologists of the Alaska Department of Fish and Game indicate that the magnitude of cutbacks described in this paper would not affect the ability of the salmon fishing fleet to harvest at the maximum sustainable yield level (Jackman et al. 1973).

Base Period for Determining Total Exvessel Revenue

In the salmon fisheries total revenue fluctuates widely from year to year depending upon the size of the salmon runs and the price paid fishermen. In the analysis, the 5-yr period from 1969 to 1973 was used as the base period for determining the total revenue produced by the state's salmon fisheries. This period was used because it appears to be the most recent, reasonably representative period for which good data exist. The total catch value was adjusted for each year by the wholesale price index using 1973 as a base year.

It was assumed in estimating the total revenue produced by each fishery that regulatory decisions would seek to maintain an historical allocation among gear types. If a reduction in the size of the southeast drift gill net fleet were to occur, for example, it is assumed that no attempt would be made to reduce the percentage of the total catch available to this fishery. It was also assumed that gear reductions in one fishery would not be made without considering the effect on catches by other fisheries utilizing the same stock. For example, a large reduction in the Cook Inlet drift gill net fishery could lead to increased catches in the set gill net fishery if it is not reduced in some reasonable proportion.

Fixed and Variable Costs

Fishing costs include such standard items as fuel, food, repairs, moorage, administrative costs, and so forth. Average costs in each fishery were collected by means of a survey in spring 1974 (Owers 1974). For vessels fishing in several fisheries, costs were prorated among each fishery based upon the length of time fished and percent of total earnings received. Other items were specifically allocated, such as gear repairs.

Because there is presently so much excess capacity in the harvesting segment of the Alaska salmon fishery, it was assumed that the total cost of harvesting the resource was a linear function of the number of boats in the fishery. This logic is used in Equations (2), (3), and (4). While this might appear to be inconsistent with economic theory because fish production would be increased for each operating unit without increasing any factor of production, in reality it is likely that costs would decrease even faster than the number of operating units leaving the fishery. This is because overcrowding in the salmon fisheries involves frequent delays in setting nets and tangled gear, and forces operators to travel long distances to make all openings. Should substantial reductions take place in a fishery, consideration of increasing costs per boat would be necessary.

Depreciation has been standardized for all vessels to a 30-yr straight line writeoff with no salvage value. Depreciation for set net sites is standardized with a 10-yr writeoff since most equipment includes small skiffs and outboard motors with a shorter useful life span.

Labor Costs

Labor costs in the fisheries are determined by a share system and fluctuate directly in proportion to gross earnings. Crew shares are ordinarily computed before bonus payments are made to the boat operator. In the analysis, it was assumed that the entire bonus was kept by the entry permit holder, which is the logic used in Equation (2). Labor costs, as used here, do not include a return to the entry permit holder's own labor.

Capital Costs

The opportunity cost of capital is assumed to be 10% and is the constant value used in Equation (3). The estimated market value of each operating unit was used in determining capital investment in the fishing business. Average market values of vessels, equipment, and fishing gear were derived for each fishery by survey. It was found in surveys conducted by the British Columbia License Control Program that the true market value of vessels averaged about 84% of the estimated value supplied by fishermen (Campbell[6]). In this analysis it was assumed that the market value of investment was 85% of the value estimated by fishermen in the survey. This is the constant value used in Equation (3) to deflate the estimated value of investment.

In addition to vessels and gear, the capital investment in the freely transferable entry permit was included in estimating total capital costs. Theoretically the permit value might be calculated by discounting future cash flows or some

[6]Campbell, B. A. 1973. A review of the development of the buy-back program and its impact on the salmon fishery. Fish. Serv., Vancouver, B.C., 54 p.

other method of determining future benefits. The problem with this approach is that it involves making implicit assumptions about the worth of the operator's own contribution of labor and management and deducting this as an expense. As an approximation of permit value, it was assumed that the permit value would equal 2 years' net earnings for those remaining in the fishery, but further research is needed to determine actual values and the relationship between price and productivity. A preliminary survey of permit values after 6 mo of limited entry indicates permits may not be worth as much as the values used here (Anonymous 1975). Using the above relationship in Equation (3), however, the permit value will increase as the number of permits is reduced and capital costs per boat will rise.

Outside Earnings

Outside earnings come principally from two sources: earnings in other fisheries and earnings from nonfishing employment. Information on average earnings from outside employment for a randomly selected sample of gear operators who fished in 1971 and 1972 was provided by the Internal Revenue Service in a format which did not disclose individual identities (Anonymous[7]).

Data on earnings from other fisheries were extrapolated from fish price data, landing statistics, and by survey. It was assumed in the analysis that outside earnings in other fisheries would not be affected by limited entry and would remain constant, except in those instances where other fisheries produced a net loss. In those cases it was assumed that a fisherman would break even in other fisheries and the value of net earnings from other fisheries would be zero.

No data have been collected to determine how much gear operators may have earned as crewmembers in other fisheries, but it is not likely that this is a substantial amount since a fisherman responsible for a vessel in one fishery is most likely the operator in other fisheries as well. No reliable data has been collected on incomes of spouses, investment earnings, transfer payments, and pensions, so no estimates were included.

[7]Anonymous. 1975. Data collection and analysis necessary to limit entry in Alaska's salmon fisheries. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., contract 03-4-208-262, Juneau, 75 p.

Fraction of Permits Issued That Are Used

Because there is no requirement that a fisherman use his entry permit every fishing season, it can be expected that not all outstanding permits will be fished.

In the analysis, the fraction of gear licenses sold to gear licenses fished during the period from 1969 to 1972 was taken as the fraction of entry permits that would be used. It will be important to monitor actual rates of participation from year to year to establish more meaningful figures.

Examples of Estimates

Using the equations and input data discussed above, tables similar to that shown in Table 2 for the southeast Alaska purse seine fishery were prepared for all those salmon fisheries which had entry limited in 1974. In each fishery, returns were first calculated using the present number of entry permits issued in that fishery. Returns were then calculated for a hypothetical reduction in the number of outstanding permits by 5% increments of the total number issued. No calculations were prepared for greater than a 45% reduction in permits because many of the assumptions discussed above would probably no longer prove correct. Table 3 shows the four estimates of returns with the present number of entry permits in each of the fisheries considered.

OPERATING UNITS NECESSARY TO ACHIEVE REASONABLE RETURNS

Once expected returns with various numbers of

TABLE 2.—Expected returns in the southeast purse seine fishery with the present number of entry permits and reductions in the number by 5% increments. No estimates have been made for greater than a 45% reduction in the number of entry permits. Similar data was prepared for all those fisheries which had entry limited in 1974.

Number of permits	Expected gross earnings	Net earnings	Net earnings less interest at 10%	Total annual income from all sources
395	$33,933	$ 9,468	$ 3,388	$21,013
375	35,719	10,507	4,219	22,052
356	37,703	11,662	5,143	23,207
336	39,921	12,953	6,175	24,498
316	42,416	14,405	7,337	25,950
296	45,244	16,050	8,653	27,595
277	48,475	17,931	10,158	29,476
257	52,204	20,101	11,894	31,646
237	56,555	22,632	13,919	34,177
217	61,696	25,624	16,313	37,169

TABLE 3.—Estimated earnings per operating unit by fishery with the present number of entry permits.

Fishery	Gross return	Net return per entry permit holder with no allowance for capital costs	Net return per entry permit holder with opportunity capital cost of 10%	Total annual income from all sources per entry permit holder
Purse seine:				
Southeastern	$33,933	$9,468	$3,388	$21,013
Prince Wm Sound	20,702	5,582	2,143	10,726
Cook Inlet	11,303	1,056	−958	8,006
Kodiak	18,096	5,655	2,365	10,340
Chignik	34,939	10,683	3,925	12,690
Peninsula-Aleutians	18,515	10,593	7,337	23,357
Drift gill net:				
Southeastern	14,346	9,019	5,177	15,614
Prince Wm Sound	7,770	2,894	1,291	5,679
Cook Inlet	6,298	2,477	905	5,567
Peninsula-Aleutians	11,862	6,990	4,039	10,086
Bristol Bay	9,821	4,210	2,504	7,588
Set gill net:				
Yakutat	3,870	940	53	2,572
Prince Wm Sound	5,469	2,539	1,332	6,079
Cook Inlet	3,102	172	−561	4,046
Kodiak	3,173	583	−225	2,094
Peninsula-Aleutians	6,115	4,630	3,337	4,948
Bristol Bay	1,993	972	628	1,445
Power troll:				
Statewide	6,820	1,432	−650	4,873

operating units have been estimated, it is possible to compare these figures with similar data from other sectors of the economy. This provides some indication of the magnitude of cutbacks in fleet size that may be necessary to achieve similar earnings in the fisheries.

Comparison With Wages Earned in a Similar Industry

As a minimum, the average rate of return should be sufficient to cover all normal operating expenses, labor costs besides those of the operator, depreciation, and a minimum return on investment of about 10%. An amount less than this indicates that the average return to the operator's labor is actually zero or less than zero. As Table 3 shows, with the present number of operating units, returns in the Cook Inlet and Kodiak set net fisheries, the Cook Inlet purse seine fishery, and the power troll fishery are not adequate. In these four fisheries, returns under this assumption were negative.

It is reasonable to expect, however, that the fisheries should provide some wage for the operator's physical labor and ability to work with mechanical equipment under hazardous working conditions. The contract construction industry is similar to the fisheries in this respect, as well as the fact that work is highly seasonal and characterized by long periods of unemployment. The comparison used here assumes that a fisherman should earn a wage equal to that of a worker in the contract construction industry during the time he is actually fishing.

The time spent in each fishery was derived by an examination of the dates of fish landings. The number of weeks shown in Table 3 represents the typical maximum length of the season between 1969 and 1972. It is recognized that not all boats fish every opening in a season, but these figures also make no allowance for the time spent preparing vessels and gear, travelling to the fishing grounds prior to the season, or time spent storing and repairing gear at the close of the season. For this reason the figures are probably somewhat conservative. Prior to the construction boom created by the Alaska pipeline, the 1973 average weekly earnings of workers in the contract construction industry in Alaska was $378 per week (Anonymous 1973b). Table 4 shows the average wage earned in the construction industry in a period of time equal to the length of the fishing season. This is compared with the number of operating units that would provide an equal rate of return to the fisherman; which can then be compared to the number of operating units now licensed.

None of the large set net fisheries or the power troll fishery are capable of earning a comparable rate of return with even a 45% reduction of entry permits. The southeast and peninsula drift gill net fisheries would require some reduction and the other drift gill net fisheries including Bristol Bay, Cook Inlet, and Prince William Sound would require substantial reductions. The purse seine

TABLE 4.—Number of permits required to produce reasonable returns assuming earnings from fishery considered are equal to wages paid in an equal time period in contract construction. The average wage in contract construction in 1973 was $378 per week.

Fishery	Length of fishing season (weeks)	Average wage paid in equal time period in contract construction	No. of permits that would provide an equal return	Present no. of permits
Purse seine:				
Southeastern	14	$5,292	356	395
Prince Wm Sound	10	3,780	202	238
Cook Inlet	10	3,780	[1]37	68
Kodiak	12	4,536	258	368
Chignik	12	4,536	76	80
Peninsula-Aleutians	12	4,536	[2]111	111
Drift gill net:				
Southeastern	22	8,316	362	453
Prince Wm Sound	19	7,182	[1]281	511
Cook Inlet	9	3,402	327	545
Peninsula-Aleutians	13	4,914	147	155
Bristol Bay	11	4,158	1,252	1,669
Set gill net:				
Yakutat	17	6,426	[1]83	150
Prince Wm Sound	9	3,402	21	32
Cook Inlet	15	5,670	[1]377	686
Kodiak	12	4,536	[1]101	183
Peninsula-Aleutians	14	5,292	54	77
Bristol Bay	9	3,402	[1]442	803
Power troll:				
Statewide	23	8,692	[1]492	895

[1]Reasonable returns cannot be achieved with a 45% reduction in entry permits.
[2]Reasonable returns can be achieved with the present number of entry permits.

fisheries, with the exception of Cook Inlet, are capable of providing a comparable rate of return with either the present maximum number or a modest reduction.

Comparison With Total Annual Earnings of Nonfarm Workers

An equally important objective of limited entry may be to bring the total income of fishermen up to levels comparable to the average earned by all workers in Alaska. It has been tacitly accepted that earnings in the fisheries, particularly in areas where few other employment opportunities exist, can be lower than in other segments of the State's economy. The continuation of this policy in the future probably makes little sense. As Alaska's economy develops, a more reasonable approach is to provide vocational training to residents of the State in areas of traditionally high unemployment so they can find employment in other sectors of the economy. If this approach is not adopted, it can be expected that job openings in the future will continue to be filled by trained persons from outside the State. In achieving increased incomes from the fisheries it should also be pointed out that a reduction in entry permits under the Alaska law will be achieved through a voluntary buy back of permits and vessels spread over as many as 10 yr. Thus, older persons in the fisheries that would have trouble finding other employment need not be displaced. Furthermore, a person who voluntarily sells to a buy-back program will receive a cash settlement that will ease the transition period.

A comparison can be made with the average incomes earned in other employment in Alaska. Estimates of total income include income from other fisheries and nonfishing employment. Because of the seasonal nature of salmon fishing, it is anticipated that many permit holders will continue to seek other employment when it is available.

Statistics collected by the Alaska Department of Labor show that average nonagricultural wage and salary earnings in 1973 were $1,006/mo, or $12,072/yr (Anonymous 1973b). Table 5 compares the number of operating units in each fishery that would be required to provide fishermen with a level of earnings equal to the state average. It is assumed that any increase in earnings will come from the particular fishery being examined.

With the exception of the small Prince William Sound set net fishery, none of the set net fisheries, the Cook Inlet and Prince William Sound drift gill net fisheries, or the power troll fishery could provide this level of income with even a 45% reduction of entry permits. The purse seine fisheries, with the exception of Cook Inlet, and the southeastern and peninsula drift gill net fisheries would provide a reasonable income with either the present number of operating units or a modest reduction.

TABLE 5.—Number of permits required to produce reasonable returns assuming the total annual income from all sources of fishermen is equal to the average earnings of nonfarm wage and salaried workers in Alaska in 1973. Nonfarm wage and salaried workers earned $12,072 in 1973.

Fishery	No. of permits required to provide total annual income of $12,072	Present no. of permits
Purse seine:		
Southeastern	[1]395	395
Prince Wm Sound	[1]214	238
Cook Inlet	41	68
Kodiak	313	368
Chignik	[1]80	80
Peninsula-Aleutians	[1]111	111
Drift gill net:		
Southeastern	[1]453	453
Prince Wm Sound	[2]281	511
Cook Inlet	[2]300	545
Peninsula-Aleutians	132	155
Bristol Bay	918	1,669
Set gill net:		
Yakutat	[2]83	150
Prince Wm Sound	19	32
Cook Inlet	[2]377	686
Kodiak	[2]101	183
Peninsula-Aleutians	[2]42	77
Bristol Bay	[2]442	803
Power troll:		
Statewide	[2]492	895

[1]Reasonable returns can be achieved with the present number of entry permits.
[2]Reasonable returns cannot be achieved with a 45% reduction in entry permits.

TABLE 6.—Number of permits required to produce reasonable returns assuming expected gross earnings equal necessary gross earnings as estimated by fishermen.

Fishery	Reasonable gross return estimated by fishermen (thousands)	No. of permits required to provide equal level of earnings	Present no. of permits
Purse seine:			
Southeastern	$31.9	[1]395	395
Prince Wm Sound	26.9	178	238
Cook Inlet	24.2	[2]37	68
Kodiak	32.8	202	368
Chignik	39.5	72	80
Peninsula-Aleutians	12.2	[1]111	111
Drift gill net:			
Southeastern	22.6	294	453
Prince Wm Sound	19.6	[2]281	511
Cook Inlet	14.5	[2]300	545
Peninsula-Aleutians	17.9	101	155
Bristol Bay	16.4	1,001	1,669
Set gill net:			
Yakutat	14.9	[2]83	150
Prince Wm Sound	14.9	[2]18	32
Cook Inlet	14.9	[2]377	686
Kodiak	11.1	[2]101	183
Peninsula-Aleutians	7.8	62	77
Bristol Bay	12.4	[2]442	803
Power troll:			
Statewide	15.3	[2]492	895

[1]Reasonable returns can be achieved with the present number of entry permits.
[2]Reasonable returns cannot be achieved with a 45% reduction in entry permits.

Comparison With Estimates Provided by Fishermen

In addition to the two measures discussed so far, as part of a survey fishermen were asked to estimate what they needed to gross from fishing in a particular year in order to earn a reasonable return (Owers 1974). In Table 6 the mean value of responses for each fishery is shown with the corresponding number of entry permits that would yield an equal level of gross earnings.

In the power troll fishery, all the set gill net fisheries with the exception of the Alaska Peninsula, the drift gill net fisheries in Prince William Sound and Cook Inlet, and the Cook Inlet purse seine fishery, it would not be possible to earn a level of earnings considered reasonable by fishermen with even a 45% reduction in entry permits.

Several other fisheries would need some reduction in the amount of gear. The purse seine fisheries in southeastern, Chignik, and the Alaska Peninsula appear capable of earning a reasonable return with either the present number of entry permits or a slight reduction.

SUMMARY BY FISHERY OF THE COMPARISONS USED

It will be noticed in Table 7 that the three comparisons used provide an estimate of the optimum number of entry permits that falls within a fairly narrow range. The following summarizes the economic performance by type of fishery.

Purse Seine

Purse seining in general appears to be the most economically viable of the four types of salmon gear fished. This is due in part to the fact that purse seiners are used in a variety of fisheries, which allows overhead expenses to be spread, and minimizes risks in any one fishery. As can be seen in Table 1, this is particularly true of the purse seine fisheries in the Alaska Peninsula and southeastern Alaska where a substantial percentage of gross earnings comes from other fisheries. The Prince William Sound and Kodiak purse seine fisheries could justify a modest reduction, although income levels would be only slightly reduced with the present maximum number. The Cook Inlet purse seine fishery, which is restricted to a hand purse seine fishery, does not appear able to provide a reasonable return with the present number of entry permits under any of the criteria.

Drift Gill Net

Unlike the purse seine fishery, the typical vessel

TABLE 7.—Number of entry permits required to produce reasonable earnings—summary of three measures.

Fishery	Return to gear operator equal to average wage in contract construction	Total annual income of gear operator equal to annual income of nonfarm wage and salaried workers	Reasonable earnings estimated by fishermen	Present no. of permits
Purse seine:				
Southeastern	356	[1]395	[1]395	395
Prince Wm Sound	202	214	178	238
Cook Inlet	[2]37	41	[2]37	68
Kodiak	258	313	202	368
Chignik	76	[1]80	72	80
Peninsula-Aleutians	[1]111	[1]111	[1]111	111
Drift gill net:				
Southeastern	362	[1]453	294	453
Prince Wm Sound	[2]281	[2]281	[2]281	511
Cook Inlet	327	[2]300	[2]300	545
Peninsula-Aleutians	147	132	101	155
Bristol Bay	1,252	918	1,001	1,669
Set gill net:				
Yakutat	[2]83	[2]83	[2]83	150
Prince Wm Sound	21	19	[2]18	32
Cook Inlet	[2]377	[2]377	[2]377	686
Kodiak	[2]101	[2]101	[2]101	183
Peninsula-Aleutians	54	[2]42	62	77
Bristol Bay	[2]442	[2]442	[2]442	803
Power troll:				
Statewide	[1]492	[2]492	[2]492	895

[1]Reasonable returns can be achieved with the present number of entry permits.
[2]Reasonable returns cannot be achieved with a 45% reduction in entry permits.

used in the drift gill net fisheries is not generally used in other fisheries besides salmon. In the southeast drift gill net fishery the present level of income appears adequate. All measures indicate that the Prince William Sound and the Cook Inlet drift gill net fisheries require a reduction in the number of entry permits. With a 45% reduction, total income and a reasonable gross income as estimated by fishermen cannot be achieved.

The Alaska Peninsula drift gill net fishery would require a reduction under all three measures examined, although substantial reductions are not required.

The Bristol Bay drift net fishery would also require a gear reduction under all of the criteria examined.

Set Gill Net

Returns in all of the set net fisheries are extremely low. The Kodiak and Cook Inlet set net fisheries cannot provide a rate of return sufficient to cover operating and capital costs. All the measures discussed indicate a 45% reduction or more. The other set net fisheries in the State would require substantial reductions in the number of entry permits.

Other data collected indicate that the set net fisheries have a rapid rate of license turnover from year to year, a high percentage of casual fishermen who participate only a few weeks out of the season, and many fishermen with low income dependence on commercial fishing (Owers 1975).

Power Troll

Returns in the power troll fishery appear inadequate to cover any of the measures discussed with a 45% reduction in permits. The fishery again cannot provide a rate of return sufficient to cover all expenses.

The power troll fishery is similar to the set net fisheries in that there is a large license turnover from year to year, and fishermen show relatively little dependence on commercial fishing for a source of income.

CONCLUSION

In many salmon fisheries it appears that restricting or reducing the number of operating units will enable earnings to rise to levels comparable to that earned in other sectors of Alaska's economy. This is probably not a practical objective in other fisheries, however, particularly the set net fisheries and the power troll fishery. This does not imply that limited entry is not necessary in these fisheries. Limited entry is still a desirable policy for management reasons and the fact that reducing or stabilizing the number of operating units in other fisheries in the same area could

result in increased catches by these fisheries if they are not limited.

Rather, the problem that must be faced is one of resource allocation. If a commercial fishery cannot be made a viable economic enterprise, the public interest to be served by allowing it to exist at all must be carefully examined. This is particularly relevant in such areas as Cook Inlet and southeastern Alaska where sport fishing is in many cases in direct competition with the commercial fisheries for a share of the resource. The fisheries are a valuable asset that belong to all the people of a state and allocation decisions must be made with this in mind.

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ABUNDANCE AND POTENTIAL YIELD OF THE ATLANTIC THREAD HERRING, *OPISTHONEMA OGLINUM*, AND ASPECTS OF ITS EARLY LIFE HISTORY IN THE EASTERN GULF OF MEXICO[1]

EDWARD D. HOUDE[2]

ABSTRACT

Eggs and larvae of the Atlantic thread herring, *Opisthonema oglinum*, were collected in plankton surveys from 1971 to 1974 in the eastern Gulf of Mexico to determine spawning seasons, spawning areas, adult biomass, and potential yield to a fishery. Aspects of the early life history also were studied. Spawning occurred from February to September, but mostly from April through August, when surface temperatures were 22.5° to 30.3°C and surface salinities ranged from 32.4 to 36.8‰. Most spawning took place from the coastline out to the 30-m depth contour, and virtually all spawning occurred where depths were less than 50 m. The area of heaviest spawning was between latitudes 26°00′N and 28°00′N. The most reliable estimates of adult biomass were approximately 110,000 metric tons in 1971 and 370,000 metric tons in 1973. The most probable estimates of potential annual yield range from 60,300 to 120,600 metric tons. Based on the best larval mortality estimates, more than 99% mortality occurred from time of spawning until 19 days and 15.5 mm standard length in 1973, and approximately 98% mortality occurred for the same period in 1971.

The Atlantic thread herring, *Opisthonema oglinum* (Lesueur), is an underexploited clupeid fish that occurs widely in the western Atlantic from southern Brazil to the Gulf of Maine (Berry and Barrett 1963), but is mainly tropical and subtropical in its distribution (Hildebrand 1963). It is a coastal species that seldom occurs in depths greater than 90 m and is most abundant in depths less than 35 m (Klima 1971). In the Gulf of Mexico it is abundant and its fishery potential has been recognized for many years (Butler 1961; Reintjes and June 1961; Bullis and Carpenter 1968; Fuss et al. 1969; Houde 1973a). The total western Atlantic thread herring catch was 12,016 metric tons in 1974 (Food and Agriculture Organization 1975), of which 2,434 metric tons were landed by the United States. Some thread herring are landed as incidental catches by both Atlantic and Gulf of Mexico menhaden fleets (Klima 1971). Catch statistics are poor for thread herring in the Gulf of Mexico, but only 435 tons were reported in 1973 (Johnson 1974). However, 5,000 tons were landed from the eastern Gulf during a 4-mo period in 1967 when a preliminary attempt was made to establish a directed fishery. Based on school sightings and catch rates by commercial purse seiners, Bullis and Thompson (1967) roughly estimated that the total Gulf of Mexico thread herring stock might be 1×10^6 tons.

Eggs and larvae of thread herring have been described (Richards et al. 1974) and the species has been successfully reared from egg to juvenile under laboratory conditions (Richards and Palko 1969). There was no information on thread herring eggs or larvae from the eastern Gulf prior to my research. Kinnear and Fuss (1971) reported seasonal north-south migrations and distribution of thread herring in the eastern Gulf of Mexico, while Fuss et al. (1969) presented data on age, growth, maturity, and food habits of that stock. Fecundity of thread herring in the eastern Gulf was determined by Prest[3] and by Martinez (1972) for fish collected on the Florida Atlantic coast.

The objective of this research was to obtain a fishery-independent estimate of the abundance and potential yield to fisheries of thread herring in the eastern Gulf of Mexico based on annual surveys of eggs and larvae during 1971 to 1974. In addition, information was obtained on spawning seasons and areas, as well as on aspects of their early life history in the eastern Gulf.

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METHODS

Adult biomass was determined from estimates of annual abundance of spawning products, a knowledge of the mean relative fecundity of thread herring, and an assumed sex ratio of 1:1 (Saville 1964; Ahlstrom 1968). Methods to determine thread herring egg and larval abundance, distribution, adult biomass, potential yield to a fishery, and mortality during egg and larval stages were analogous to methods reported in detail for round herring (Houde 1977a). Other details of survey design and planning also have been published (Rinkel 1974; Houde and Chitty 1976; Houde et al. 1976). Temperature and salinity data, as well as some egg and larvae data, from these surveys are stored in the National Oceanographic Data Center, Washington, D.C., under the MAFLA file.

The survey area was located on the broad continental shelf off western Florida in the eastern Gulf of Mexico, between lat. 24°45′N and 30°00′N (Figure 1). In 17 cruises (Table 1) from 1971 to 1974, plankton was collected with a 61-cm bongo net sampler fitted with 505- and 333-μm mesh nets. Most stations were over water depths from 10 to 200 m, except in 1974 when some stations as shallow as 5 m were added to the sampling plan. These shallow stations were added to determine if thread herring and scaled sardine, *Harengula jaguana*, spawning increased significantly nearshore where there had been no previous sampling. Thread herring eggs and larvae were identified using descriptions by Houde and Fore (1973) and by Richards et al. (1974).

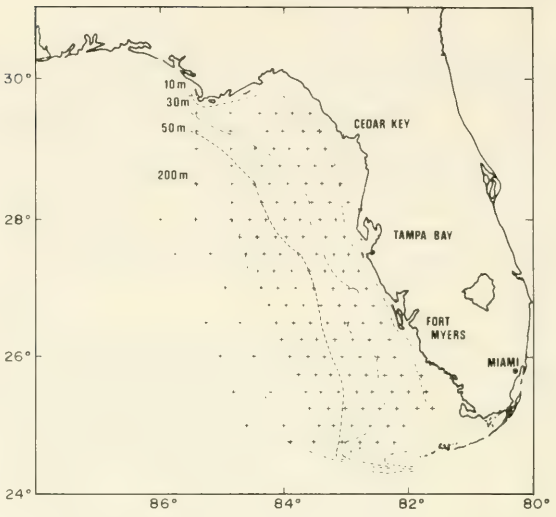

FIGURE 1.—Area encompassed by the 1971–74 eastern Gulf of Mexico ichthyoplankton surveys. Plus symbols (+) represent stations that were sampled during the survey. The 10-, 30-, 50-, and 200-m depth contours are indicated.

Egg and larval abundances at stations in the cruise area, over the time period represented by a cruise, and on an annual basis, were estimated using techniques similar to those outlined by Sette and Ahlstrom (1948), reviewed by Saville (1964), and most recently discussed by Smith and

TABLE 1.—Summarized data on cruises to the eastern Gulf of Mexico, 1971–74, to estimate abundance of thread herring eggs and larvae. GE = RV *Gerda*, 8C = RV *Dan Braman*, TI = *Tursiops*, 8B = RV *Bellows*, IS = RV *Columbus Iselin*, CL = RV *Calanus*.

Cruise	Dates	Number of stations	Positive stations for eggs[1]	Positive stations for larvae[2]	Mean egg abundance under 10 m²		Mean larvae abundance under 10 m²	
					All stations	Positive stations	All stations	Positive stations
GE7101[3] 8C7113 TI7114	1–8 Feb. 1971 7–18 May 1971	20 123	0 13	0 47	0.00 28.42	— 276.82	0.00 27.67	— 52.63
GE7117 8C7120 TI7121 TI7131 8B7132	26 June–4 July 1971 7–25 Aug. 1971	27 146	4 3	13 11	0.85 0.72	14.39 42.46	17.48 11.02	51.87 79.91
GE7127 8B7201 GE7202	7–16 Nov. 1971 1–11 Feb. 1972	66 30	0 0	0 0	0.00 0.00	— —	0.00 0.00	— —
GE7208	1–10 May 1972	30	4	14	7.98	75.92	13.61	36.08
GE7210	12–18 June 1972	13	2	10	2.11	17.09	172.28	228.36
IS7205	9–17 Sept. 1972	34	0	4	0.00	—	1.04	13.78
IS7209	8–16 Nov. 1972	50	0	0	0.00	—	0.00	—
IS7303	19–27 Jan. 1973	51	0	0	0.00	—	0.00	—
IS7308	9–17 May 1973	49	4	21	60.53	999.46	34.73	101.19
IS7311	27 June–6 July 1973	51	12	19	28.28	137.98	68.74	229.37
IS7313	3–13 Aug. 1973	50	0	10	0.00	—	6.10	40.24
IS7320	6–14 Nov. 1973	51	0	0	0.00	—	0.00	—
CL7405	28 Feb–9 Mar. 1974	36	0	5	0.00	—	0.31	2.43
CL7412	1–9 May 1974	44	10	22	13.98	75.53	30.80	57.56

[1]Positive station is a station at which thread herring eggs were collected.
[2]Positive station is a station at which thread herring larvae were collected.
[3]An ICITA 1-m plankton net was used on this cruise. On all other cruises a 61-cm bongo net was used.

Richardson (in press). Variance estimates on cruise and on annual egg abundance estimates were calculated by methods used by Cushing (1957) and Taft (1960). Houde (1977a) has given detailed procedures, including estimating formulae, that were used to obtain abundance estimates of clupeid eggs and larvae in eastern Gulf of Mexico surveys.

Two methods were used to estimate adult biomass, based on two different procedures for determining annual spawning by thread herring. The first procedure is that given by Sette and Ahlstrom (1948). The estimate of annual spawning depends on integrating station and cruise estimates over area and time. The second procedure is based on a modification of Simpson's (1959) method in which annual spawning is estimated by plotting the daily spawning estimates for each cruise against the middate of the cruise and then determining the area under the resulting polygon by planimetry.

Potential Yield to a Fishery

Houde (1977a) used the estimator suggested by Alverson and Pereyra (1969) and Gulland (1971, 1972) to predict potential yield of round herring in the eastern Gulf. The same procedure was used for thread herring. The estimating formula is $C_{max} = XMB_0$ where X is assumed to equal 0.5, M is the natural mortality coefficient, and B_0 is the virgin biomass. My biomass estimates are estimates of B_0 since the thread herring stock is virtually unfished in the eastern Gulf. Because no estimate of M exists for thread herring, the potential annual yield was predicted using a range of probable values of the mortality coefficient.

Larval Abundance and Mortality

Mortality estimates were determined for larvae by length and by estimated ages. The exponential decrease in abundance of 1-mm length classes was used to calculate mortality coefficients to describe the decline in catches by length. Growth was assumed to be exponential during the larval phase. Based on this assumption and information on laboratory growth rates for thread herring larvae, ages of larvae in 1-mm length classes were estimated. Mortality coefficients were then estimated from the decline in abundance of larvae in relation to estimated age. Houde (1977a) gave estimating formulae and discussed the rationale for his procedures, which are similar to those used previously by Ahlstrom (1954) and Nakai and Hattori (1962).

RESULTS AND DISCUSSION

Occurrence of Eggs and Larvae

Thread herring eggs occurred in 8 of the 17 cruises from 1971 to 1974, and larvae occurred during 11 of the cruises (Table 1). Eggs were collected on cruises from May through August, although significant spawning may have occurred during April when no cruises were scheduled. Some larvae were collected as early as March and as late as September, but they were most abundant from May through August. No eggs or larvae were collected from September through January. Fuss et al. (1969) reported ripe or nearly ripe adult thread herring from the eastern Gulf in March through August. My data support their finding that thread herring spawning is confined to spring and summer in this area.

Most spawning takes place within 50 km of shore on the inner continental shelf in depths <30 m, and virtually all spawning occurs within 100 km of shore at depths <50 m (Figure 2). A single instance of egg occurrence beyond the 50-m depth contour was recorded (Figure 2). Spawning was most intense between lat. 26°00′N and 28°00′N, the area from just south of Fort Myers to Tampa Bay, Fla. This is the area where an attempt was made to establish a commercial fishery for thread herring in the 1960's (Fuss 1968; Fuss et al. 1969). Kinnear and Fuss (1971) found that thread herring that were concentrated near Fort Myers (lat. 26°00′N) in winter migrated north during warmer months. My egg distribution data suggest that a large part of the thread herring population remains within the Fort Myers–Tampa Bay area throughout the year.

Larval distribution was more widespread than that of eggs, presumably due to dispersal by water currents, but was generally similar to egg distribution (Figure 2). Most larvae were collected where water depths were <50 m and only six occurrences were recorded where depths were >50 m (Figures 2–6).

Thread herring eggs and larvae were relatively common in eastern Gulf ichthyoplankton. A total of 4,236 thread herring eggs were collected during the 17 cruises, 1.39% of the 304,507 total fish eggs

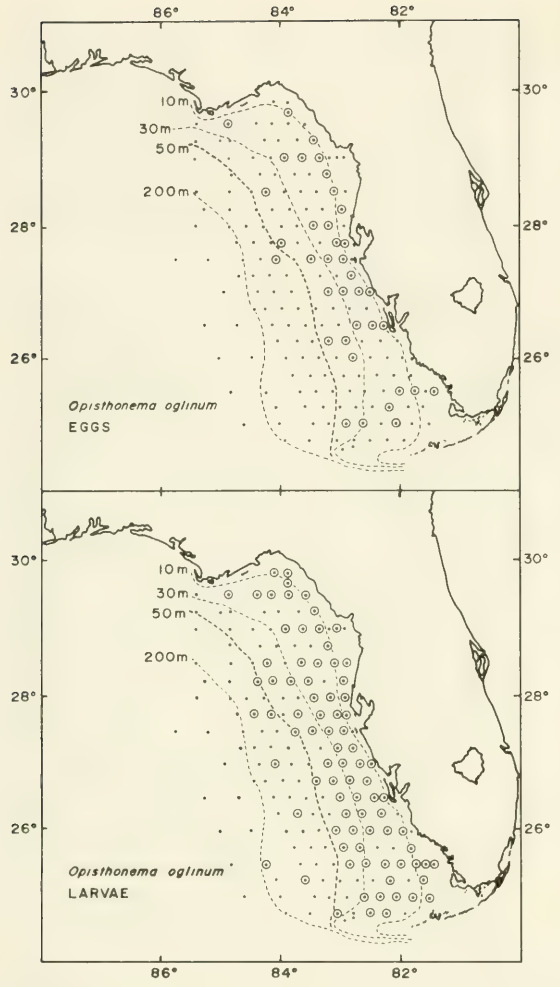

FIGURE 2.—Top. Stations in the survey area where eggs of thread herring were collected at least once during 1971–74. Stations where eggs did not occur are indicated by dots. Bottom. Stations in the survey area where larvae of thread herring were collected at least once during 1971–74. Stations where larvae did not occur are indicated by dots.

sorted from 867 samples. Number of thread herring larvae totalled 11,255, 7.87% of the 143,004 total larvae collected throughout the survey. Thread herring eggs constituted 13.20% of the total clupeid eggs collected, and thread herring larvae constituted 39.69% of the clupeid larvae.

Mean abundances of thread herring eggs under 10 m^2 of sea surface ranged from 0.00 to 60.53 for the 17 cruises (Table 1). At positive stations, cruise means ranged from 14.39 to 999.46 under 10 m^2. Most egg abundances at individual stations were <100 under 10 m^2 of sea surface, but abundances ranged from 101 to 1,000 under 10 m^2 on eight occasions and >1,000 under 10 m^2 on four occasions (Figures 3–6).

Thread herring larvae mean abundances for the 17 cruises ranged from 0.00 to 172.28 under 10 m^2 of sea surface (Table 1). At positive stations, mean cruise abundances ranged from 2.43 to 229.37 under 10 m^2. Larval abundances exceeded 1,000 under 10 m^2 on three occasions (Figures 3–6) and frequently were in the range of 101 to 1,000 under 10 m^2. Detailed summaries of station and cruise data for both larvae and eggs of thread herring were recently published (Houde et al. 1976).

Spawning intensity appeared to vary within the observed spawning area. The $\log_{10}$ mean egg abundance under 10 m^2 for positive stations from all cruises was 1.3837 at stations ≤30 m deep but was only 1.2750 at stations >30 m. The means did not differ significantly (t-test, $P>0.50$). But, the surface area encompassed by the ≤30-m depth zone was 76.03×10^9 m^2 as opposed to only 30.69×10^9 m^2 in the 30- to 50-m depth zone, beyond which virtually no spawning was observed (Figure 2). Most eggs were spawned where depth was <30 m.

There was no evidence that spawning intensity increased nearer to the coast than measured by our usual survey stations, based on cruise CL7412 (Figure 6, Table 1), when 12 nearshore stations were added to the usual stations. Thread herring eggs were collected at three of the nearshore stations and at seven of the regular, more offshore stations (Figure 6) on that cruise. The $\log_{10}$ mean catch under 10 m^2 was higher at the offshore stations, but due to the small number of stations it did not differ significantly ($P>0.10$) from the nearshore stations' mean:

Stations	*No. of stations with thread herring eggs*	*Log*$_{10}$ $\bar{x}$	*Log*$_{10}$ $S_{\bar{x}}$
Regular	7	1.5272	0.5064
Nearshore	3	0.5525	0.3101

$t_{calc} = 1.69$ $\quad t_{0.05(2,8)} = 2.306$

Temperature and Salinity Relations

Thread herring eggs were collected where surface temperatures ranged from 22.5° to 30.3°C and surface salinities from 32.4 to 36.8‰. From May to September temperatures from surface to 15 m were nearly homothermous, but temperatures at the 30-m depth often differed from the surface by

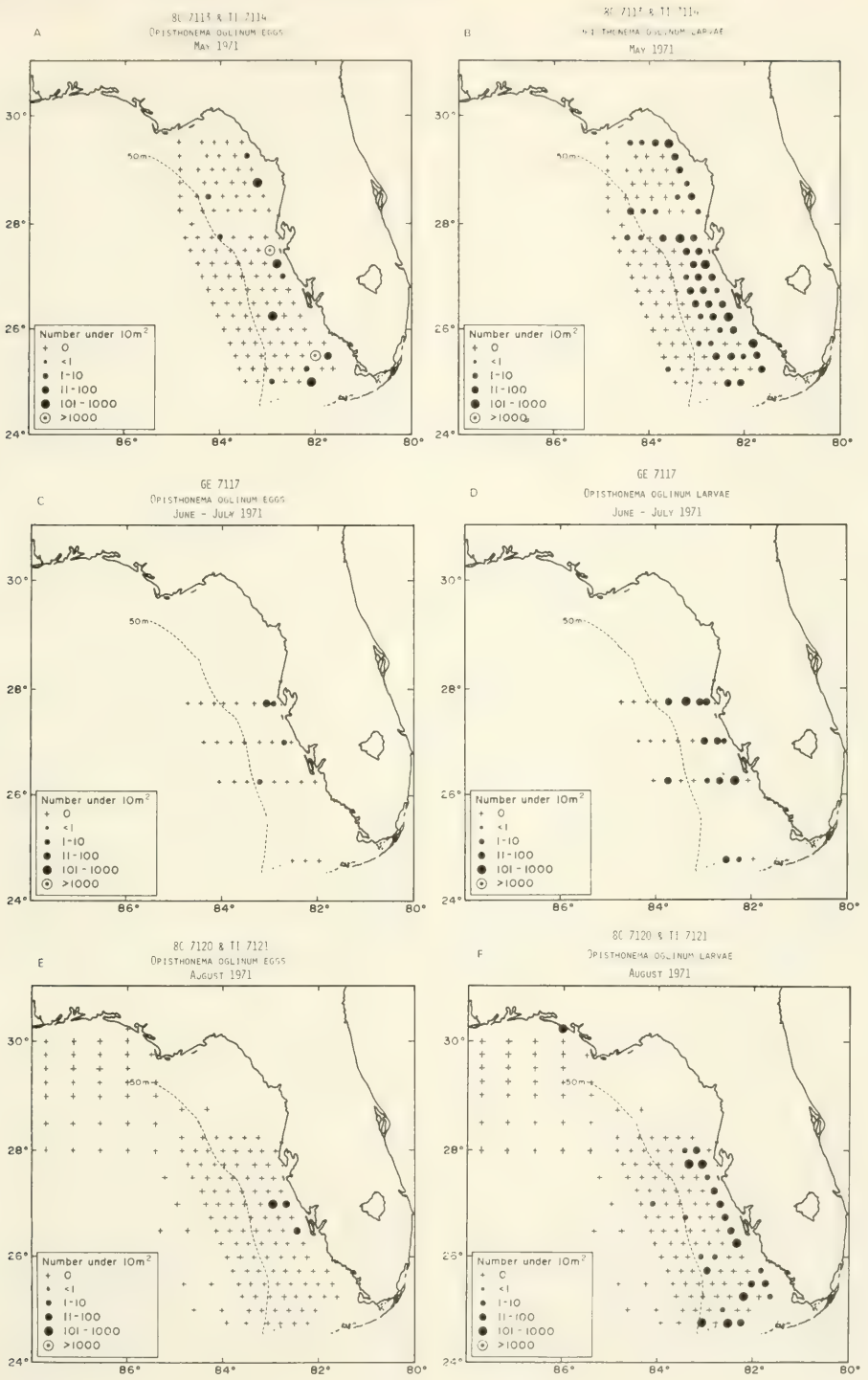

FIGURE 3.—Distribution and abundance of thread herring eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface A, B. Cruise 8C7113–TI7114, May 1971. C, D. Cruise GE7117, June–July 1971. E, F. Cruise 8C7120–TI7121, August 1971.

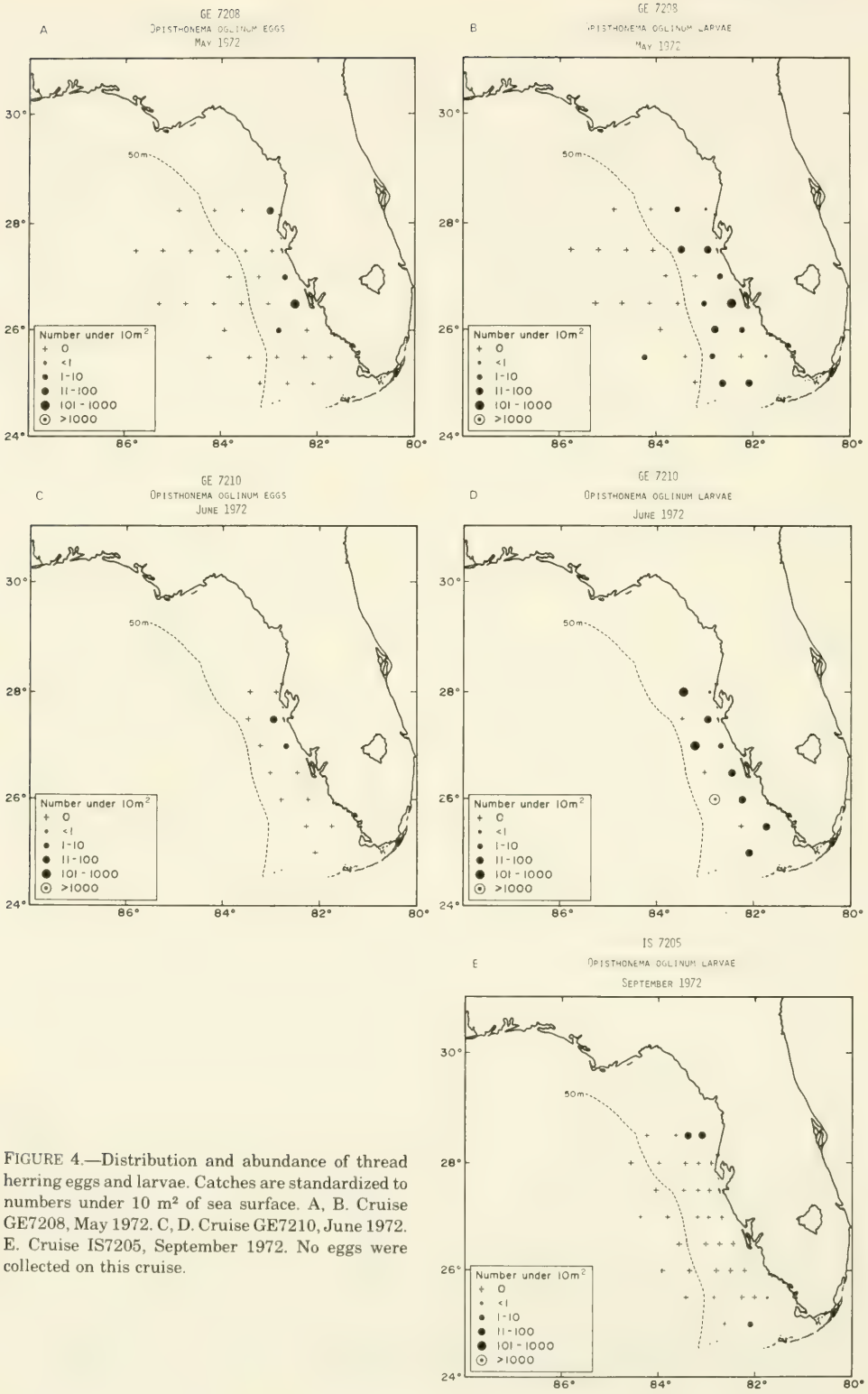

FIGURE 4.—Distribution and abundance of thread herring eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B. Cruise GE7208, May 1972. C, D. Cruise GE7210, June 1972. E. Cruise IS7205, September 1972. No eggs were collected on this cruise.

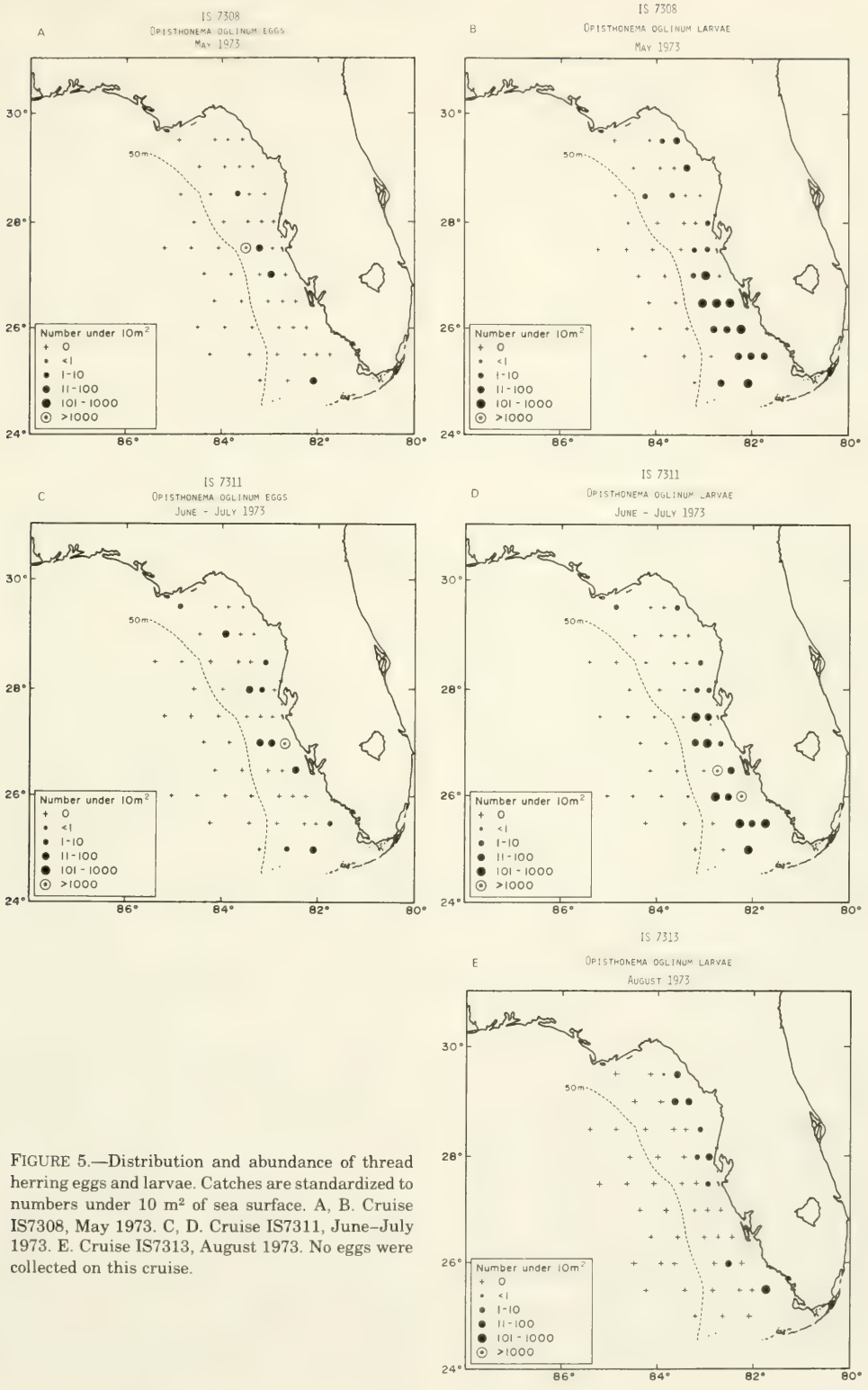

FIGURE 5.—Distribution and abundance of thread herring eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B. Cruise IS7308, May 1973. C, D. Cruise IS7311, June–July 1973. E. Cruise IS7313, August 1973. No eggs were collected on this cruise.

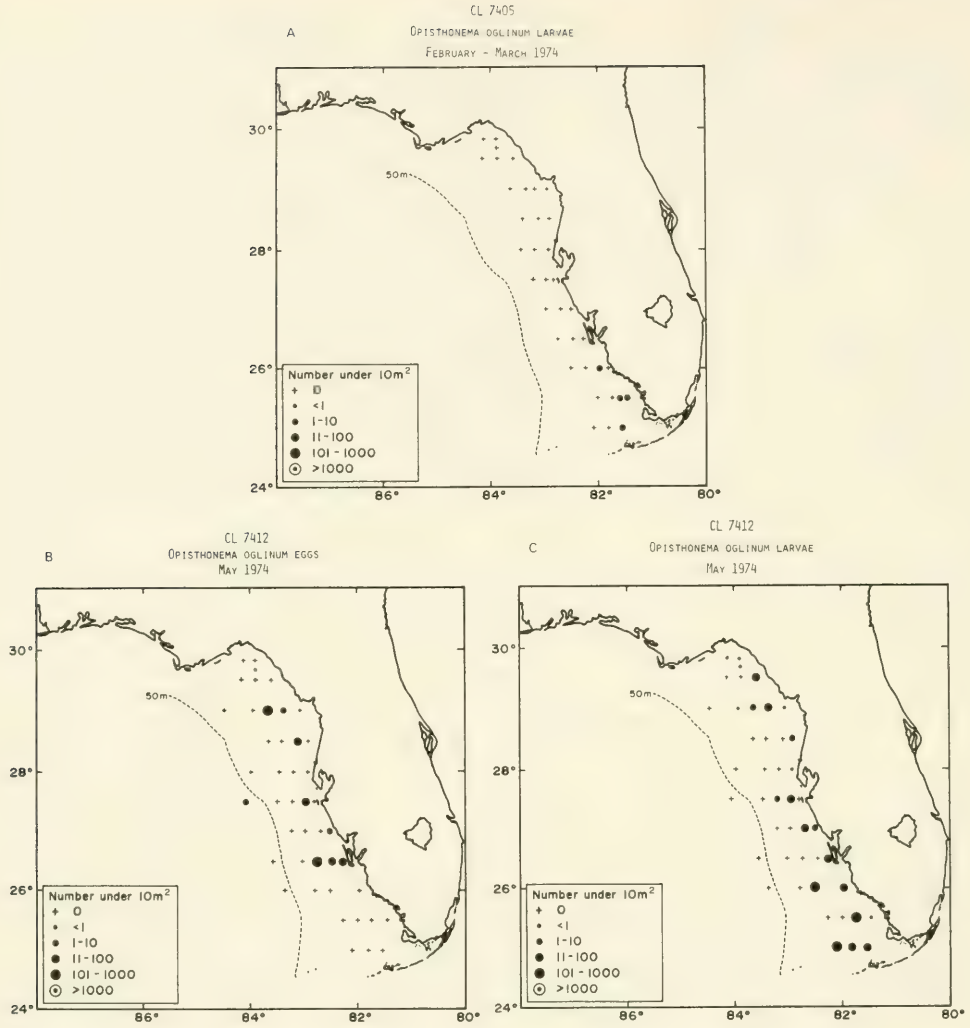

FIGURE 6.—Distribution and abundance of thread herring eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A. Cruise CL7405, February–March 1974. No eggs were collected on this cruise. B, C. Cruise CL7412, May 1974.

2° to 3°C, with a maximum difference of 5°C observed. At the 50-m depth, temperatures differed from the surface by as much as 9°C, but usually by 3° to 5°C. Because most spawning takes place at depths less than 30 m, it is unlikely that spawning and surface temperatures differed by more than 2°C. Salinity did not differ by more than 1‰ from surface to the 50-m depth, except in 1973, when surface salinities over wide areas during summer were depressed (Anonymous 1975)[4] due to Mississippi River runoff some months earlier. In 1973 salinity differences as great as 4‰ between surface and 50 m were observed in areas where some thread herring spawning occurred. Small larvae (≤5.0 mm standard length [SL]), <5 days old, were collected where surface temperatures were 18.5° to 30.9°C and salinities were 27.3 to 36.9‰. The ranges were greater for larvae than for eggs.

Based on combined 1971–74 data, most thread herring eggs and ≤5.0-mm larvae were collected at surface temperatures from 25.1° to 30.0°C (Figure 7). All stations with eggs and more than 98% of the stations with ≤5.0-mm larvae had surface temperatures above 22°C. More than 74% of the

[4]Anonymous. 1975. Compilation and summation of historical and existing physical oceanographic data from the eastern Gulf of Mexico. State Univ. Syst. Fla., Inst. Oceanogr., St. Petersburg, Fla. Final Rep. to U.S. Bur. Land Manage., Contract No. 08550-CT4-16, 97 p., 10 app.

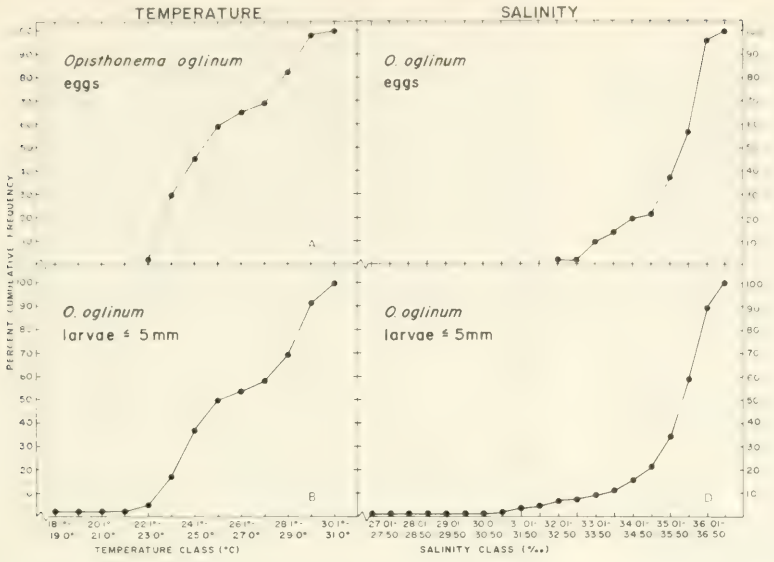

FIGURE 7.—Percent cumulative frequency distribution of 1971–74 stations where thread herring eggs occurred in relation to surface temperatures (A) and to surface salinities (C), and ≤5.0-mm SL larvae occurred in relation to surface temperatures (B) and surface salinities (D).

stations with eggs and 68% with ≤5.0-mm larvae occurred where salinity ranged from 35.0 to 36.5‰. Spawning rarely occurred at surface salinities <33‰.

Egg and Larval Abundance in Relation to Zooplankton

There was no clear relationship between abundance of thread herring eggs or larvae and zooplankton volume at stations for 12 cruises in 1972–74. Houde and Chitty (1976) determined that mean zooplankton volume from the 333-μm mesh bongo net was 153.4 cm^3/1,000 m^3 in that period. Egg abundances showed no relationship to zooplankton volumes; larvae did appear to be most abundant at stations where zooplankton volumes exceeded 153.4 cm^3/1,000 m^3. But, zero catches or low catches of larvae also were common where zooplankton volumes were high. The lack of significant correlation between larval abundance and zooplankton volume was not surprising because the 333-μm mesh does not sample zooplankton of the size eaten by small thread herring larvae.

Relative Fecundity

The mean relative fecundity of thread herring females is 594.0 ova/g ($S_{\bar{x}}$ = 29.4 ova/g), calculated from Martinez's (1972) weight and fecundity data that he obtained from nine females of 53.8 to 109.4 g. There was no apparent relationship between relative fecundity and either length or weight of the nine thread herring used in this analysis. The mean relative fecundity value was used in all subsequent biomass estimate calculations. Because mean relative fecundity with its 0.95 confidence limits is $\bar{x} = 594 \pm 68$, the maximum biomass estimating error attributable to the relative fecundity estimate is about ±11%.

Time Until Hatching

Thread herring eggs apparently hatch in <24 h at temperatures of 25° to 30°C, where most spawning takes place in the eastern Gulf. The evidence is indirect because no living thread herring eggs were available for incubation experiments. Eggs did not occur in more than one stage of development from any single sample during these surveys. Newly fertilized eggs were collected only at night, mostly from 2200 to 0200; and full-term embryos were found only during the afternoon from 1400 to 1800. I assigned a mean estimated hatching time for eggs as 0.84 days (20 h) from the evidence that was available. Thread herring eggs were rarely caught at stations sampled between the hours of 1600 and 2100, presumably because they had already hatched. Thus, abundance of thread herring eggs spawned during each cruise was underestimated. Annual spawning estimates, as well as variances, were corrected for egg stage duration (equations 4, 5; Houde 1977a) and corrected estimates were subsequently used to calculate biomasses.

Cruise Egg Abundance

The estimated abundance of thread herring eggs in the area represented by each cruise is given in Table 2. For cruises in which eggs occurred, abundances ranged from 0.86 to 91.66 $\times$ 10^{10} eggs. The Table 2 estimates, which represent abundance of eggs present on a day during a cruise, were corrected for egg stage duration and then expanded to represent the number of days encompassed by the cruise period (Sette and Ahlstrom 1948; Houde 1977a).

TABLE 2.—Abundance estimates of thread herring eggs for each cruise. Estimates were obtained using Equations (2) and (3) (Houde 1977a) and are not corrected for duration of the egg stage.

Cruise	Area represented by the cruise ($m^2 \times 10^9$)	Positive area[1] ($m^2 \times 10^9$)	Cruise egg abundance (eggs $\times 10^{10}$)
GE7101	25.79	0.00	0.00
8C7113 and TI7114	120.48	55.81	34.25
G7117	101.10	48.73	0.86
8C7120 and TI7121	189.43	26.26	1.37
GE7127, 8B7132 and TI7131	72.99	0.00	0.00
8B7201 and GE7202	148.85	0.00	0.00
GE7208	124.88	65.98	11.93
GE7210	48.43	38.93	1.02
IS7205	104.59	11.16	0.00
IS7209	149.80	0.00	0.00
IS7303	149.80	0.00	0.00
IS7308	151.42	54.09	91.66
IS7311	156.50	53.21	44.26
IS7313	153.18	21.75	0.00
IS7320	153.89	0.00	0.00
CL7405	52.00	6.70	0.00
CL7412	91.33	47.89	12.77

[1]Positive area is defined as the area representing stations where either eggs or larvae of thread herring were collected.

Adjusting Cruise Egg Abundance Estimates

Because the entire potential spawning area was not sampled on cruises GE7117, 8C7120–TI7121, GE7208, and GE7210 (Figures 3, 4), an area adjustment factor was applied to correct the egg abundance estimates in Table 2. The area adjustment factor was equal to the fraction of the potential spawning area that was sampled on a given cruise. For cruise GE7117 it was 0.404; for 8C7120–TI7121, 0.746; for GE7208, 0.746; and for GE7210, 0.753. The abundance estimate for each of those cruises (Table 2) was corrected by dividing it by its area adjustment factor. Corrected abundance estimates are: GE7117—2.12 $\times$ 10^{10}; 8C7120–TI7121—1.83 $\times$ 10^{10}; GE7208—15.98 $\times$ 10^{10} GE7210—1.36 $\times$ 10^{10}.

Annual Spawning and Biomass Estimates

Method I

Estimates of total annual spawning by thread herring in the eastern Gulf ranged from 140.528 $\times$ 10^{11} eggs in 1972 to 1,105.932 $\times$ 10^{11} eggs in 1973 (Table 3). Estimated adult biomasses were 110,024 metric tons in 1971, 47,316 metric tons in 1972, and 372,367 metric tons in 1973 (Table 3). The 1972 estimate is unreliable because a cruise that was scheduled during the peak of the spawning season was terminated before completion, due to a hurricane. The actual biomass in 1972 probably is much higher than the estimate. Consider-

TABLE 3.—Annual spawning and biomass estimates for thread herring from the eastern Gulf of Mexico during 1971, 1972, and 1973 spawning seasons. Estimates are based on the Sette and Ahlstrom (1948) technique. The 1972 estimate is unreliable because a hurricane curtailed survey cruise GE7210 during the peak of the spawning season. Details of the estimating procedure are given in Houde (1977a).

Year	Cruise	Daily spawning estimate (eggs $\times 10^{11}$)	Days represented by cruise	Eggs spawned during cruise period ($\times 10^{11}$)	Variance estimates on spawned eggs ($\times 10^{24}$)	Adult biomass (metric tons)
1971	GE7101	0.000	51.5	0.000	—	
	8C7113 TI7114	4.111	74.5	306.283	20.429	
	GE7117	0.255	44.5	11.365	8.549	
	8C7120 TI7121	0.220	41.5	9.124	1.556	
Annual total				326.772	30.534	110,024
1972	8B7201 GE7202	0.000	50.0	0.000	—	
	GE7208	1.919	65.0	124.706	47.060	
	GE7210	0.163	97.0	15.822	25.507	
Annual total				140.528	72.567	47,316
1973	IS7303	0.000	46.5	0.000	—	
	IS7308	11.004	79.5	874.802	49.839	
	IS7311	5.313	43.5	231.130	20.284	
	IS7313	0.000	42.5	0.000	—	
Annual total				1,105.932	70.123	372,367

ing only 1971 and 1973 estimates of egg abundance and their respective variances, the 0.95 confidence intervals on thread herring biomass during those years ranged from 72,814 to 428,758 metric tons.

The area adjustments that corrected egg abundance estimates for four 1971 and 1972 cruises had a relatively minor effect on biomass estimates in those years. Corrected estimates, presented in Table 3, exceeded uncorrected estimates by 3,060 metric tons in 1971 and by 11,946 metric tons in 1972.

Method II

An estimate of annual spawning also was obtained by a modification of Simpson's (1959) method (Houde 1977a). Biomasses of adult thread herring were then estimated (Table 4); they were 108,139 metric tons in 1971, 45,048 metric tons in 1972, and 325,803 metric tons in 1973.

Most Probable Biomass

If the 1972 estimates are not considered, the most likely adult thread herring biomass in the eastern Gulf during 1971–73 was between 100,000 and 400,000 metric tons. Yearly fluctuations in thread herring biomass may be significant in the eastern Gulf of Mexico but the size of such fluctuations could not be determined. Severe red tides, which are common in the area, and hurricanes are just two phenomena occurring during summer months that might affect annual recruitment, causing significant year-class fluctuations. But, during the years of this study it seems unlikely that the stock of adult thread herring exceeded 430,000 metric tons and it probably was less than that amount. These estimates represent only a part of the Gulf of Mexico thread herring population. Large sotcks exist in the northern and western Gulf that are not included in the estimates. Also, juvenile thread herring biomass is not included and it may constitute a significant part of the population that could be harvested by a fishery.

TABLE 4.—Annual spawning and biomass estimates for thread herring from the eastern Gulf of Mexico during 1971, 1972, and 1973. Estimates are based on the method described by Simpson (1959). The 1972 estimate is unreliable because a hurricane curtailed survey cruise GE7210 during the peak of the spawning season.

Year	Cruise	Daily spawning estimate (eggs $\times 10^{11}$)	Annual spawning estimate (eggs $\times 10^{11}$)	Adult biomass (metric tons)
1971	GE7101	0.000		
	8C7113			
	TI7114	4.111		
	GE7117	0.255		
	8C7120			
	TI7121	0.220		
			321.172	108,139
1972	8B7201			
	GE7202	0.000		
	GE7208	1.919		
	GE7210	0.163		
			133.793	45,048
1973	IS7303	0.000		
	IS7308	11.004		
	IS7311	5.313		
	IS7313	0.000		
			967.636	325,803

Concentration of Biomass

If thread herring adults were evenly distributed from the coastline to the 50-m depth contour in 1971 and 1973, an area of 106.7×10^5 ha, the concentration of biomass would be in the range of 6.8 to 40.2 kg/ha, based on adult biomass estimates and the 0.95 confidence interval on those estimates. The estimated thread herring biomass concentration is less than that for round herring (Houde 1977a) which ranged from 14.1 to 102.3 kg/ha. Round herring occur in a smaller area of the eastern Gulf than thread herring; the round herring being mostly confined to the 30- to 200-m depth zone which is 76.5×10^5 ha. Thread herring, although less concentrated, are highly visible because of surface schooling behavior and also are presumably more accessible to a potential fishery because they are found nearer to the coast in shallower water.

Potential Yield to a Fishery

Estimates of annual potential yield of adult thread herring from the eastern Gulf range from 27,506 to 186,184 metric tons (Table 5). Estimates were obtained from $C_{max} = XMB_0$ where M, the natural mortality coefficient, was assigned three

TABLE 5.—Range of potential yield estimates for eastern Gulf of Mexico thread herring, based on biomass estimates in 1971 and 1973 by the Sette and Ahlstrom (1948) method. Yields are predicted at three possible values of M, the natural mortality coefficient. Biomass estimates were obtained from values in Table 3.

Year	Biomass estimate (metric tons)	Estimated potential annual yields (metric tons) for given values of M		
		$M=0.5$	$M=0.75$	$M=1.0$
1971	110,024	27,506	41,259	55,012
1973	372,367	93,092	139,638	186,184
Mean of 1971 and 1973	241,196	60,299	90,448	120,598

values (0.5, 0.75, and 1.00) within the probable range for thread herring. Based on the mean of 1971 and 1973 biomass estimates, potential yield ranged from 60,300 to 120,600 metric tons. It is likely that the sustainable yield of adult stock was in that range during 1971–73. Assuming thread herring are evenly distributed within the 106.7×10^5 ha spawning area, then probable harvestable yields of adult thread herring range from 5.6 to 11.3 kg/ha. Yield could be supplemented by some additional catch of juveniles.

The eastern Gulf thread herring stock apparently is not as large as the menhaden stock in the north-central Gulf. But, a potential harvest, based on 1971–73 biomass levels, of about 100,000 metric tons substantiates the belief that thread herring are a significant resource in the eastern Gulf that could provide raw material for the fishmeal industry. Because large fluctuations in thread herring year-class strength may occur, yield in some years could be considerably higher than that predicted based on 1971–73 abundance. The potential for thread herring harvest is higher in the eastern Gulf of Mexico than that estimated along the Atlantic coast by Pristas and Cheek (1973).

Larval Abundance

Larval abundance varied seasonally with peak abundance in spring and summer months (Table 6). Abundance estimates for cruises in which thread herring larvae were collected ranged from 0.16 to 107.57×10^{10} larvae in the survey area. Thread herring larvae were collected in small numbers on three cruises in which no eggs were taken (Table 1). Cruises IS7205 and IS7313 were made in late summer when eggs, if present, must have been rare. Larvae collected in early March, during cruise CL7405, occurred only in the southernmost part of the survey area (Figure 6). They occurred at five stations on that cruise but abundances were only 0.6 to 4.4 under 10 m^2. The presence of larvae indicated that some spawning began as early as February and that it continued as late as September.

TABLE 6.—Abundance estimates of thread herring larvae for each cruise. Estimates include larvae in all size classes and were obtained using Equations (2) and (3) (Houde 1977a).

Cruise	Area represented by the cruise ($m^2 \times 10^9$)	Positive area[1] ($m^2 \times 10^9$)	Cruise larvae abundance[2] (larvae $\times 10^{10}$)
GE7101	25.79	0.00	0.00
8C7113 and TI7114	120.48	55.81	33.34
GE7117	101.10	48.73	17.67
8C7120 and TI7121	189.43	26.26	20.87
GE7127, TI7131, and 8B7132	72.99	0.00	0.00
8B7201 and GE7202	148.85	0.00	0.00
GE7208	124.88	65.98	20.36
GE7210	48.43	38.93	83.43
IS7205	104.59	11.16	1.09
IS7209	149.80	0.00	0.00
IS7303	149.80	0.00	0.00
IS7308	151.42	54.09	52.58
IS7311	156.50	53.21	107.57
IS7313	153.18	21.75	9.34
IS7320	153.89	0.00	0.00
CL7405	52.00	6.70	0.16
CL7412	91.33	47.89	28.13

[1]Positive area is defined as the area representing stations where either eggs or larvae of thread herring were collected.

[2]Values are not adjusted for cruises that did not encompass the entire area, nor have estimates been corrected to account for gear avoidance by larvae at stations sampled in daylight.

The seasonal nature of thread herring larvae abundance can be observed in plotted length–frequency distributions for each cruise in which larvae were collected (Figure 8). Larvae were represented in length classes up to 23.0 mm SL, but specimens longer than 15.0 mm were uncommon. The smallest length classes (1.1–3.0 mm) represent larvae in poor condition or that were distorted from net capture and preservation, because recently hatched thread herring larvae are 3.8 to 4.0 mm SL (Richards et al. 1974).

Fewer larvae were collected at stations sampled during the day than at night, indicating that gear avoidance was relatively great during daylight, particularly by larger larvae. The ratio of night catches to day catches increased rapidly when summed catches under 10 m^2 over all cruises were plotted for each 1-mm length class (Figure 9). No larvae longer than 17.0 mm were collected during daylight. An exponential function $R = 0.3470e^{0.2492X}$ was fitted to the plotted data for larvae up to 17.0 mm (Figure 9), where R is the ratio of night-caught to day-caught larvae and X is standard length. It provided the correction factor R (Houde 1977a), by which daytime catches were adjusted to obtain abundance estimates of larvae by 1-mm length classes in each station area on a cruise. The correction for undersampling during daylight probably did not completely account for gear avoidance by larvae (Smith and Richardson in press), but it helped to provide a better estimate of larval abundance for subsequent estimation of survival rates. The observed increase in ratio of night- to day-caught thread herring larvae throughout the larval period seems typical of clupeid larvae (Ahlstrom 1954, 1959; Lenarz 1973; Matsuura in press). But, observations on round

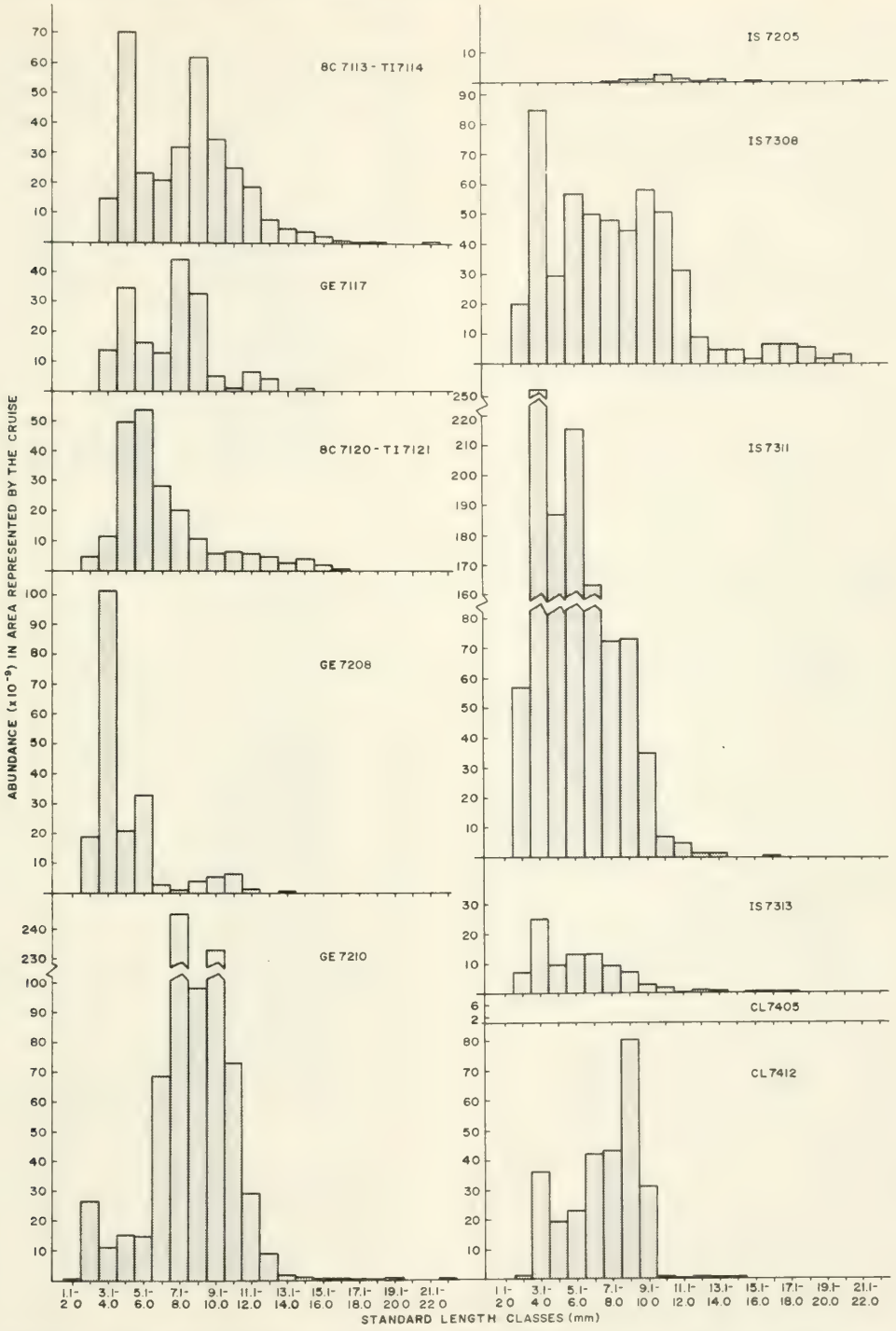

FIGURE 8.—Length–frequency distributions of thread herring larvae for 1971–74 cruises to the eastern Gulf of Mexico. Frequencies are expressed as estimated abundance of larvae in each length class within the area represented by the cruise. No adjustments for abundance have been made for cruises that did not cover the entire area where thread herring larvae might occur.

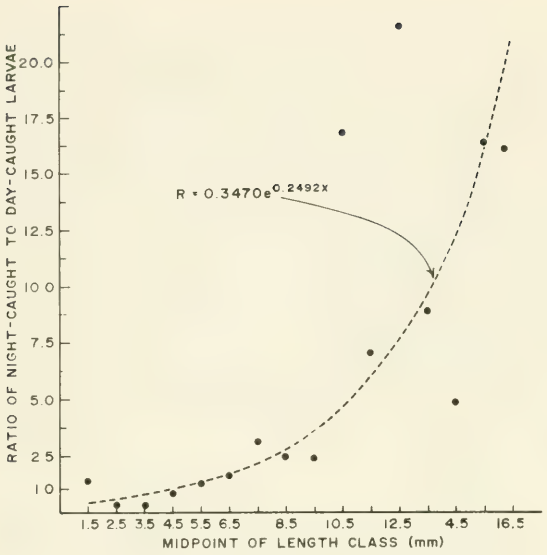

FIGURE 9.—Night to day ratios of sums of catches, standardized to numbers under 10 m² of sea surface, for thread herring larvae collected in 1971–74 in the eastern Gulf of Mexico. The ratios were calculated for larvae within each 1-mm length class from 1.1 to 17.0 mm SL. A fitted exponential regression describes the relationship. Larval abundance estimates for each length class at stations occupied during daylight were corrected by the appropriate ratio factor for each length class to account for daytime avoidance.

herring larvae (Houde 1977a) showed relative increases in night catches until larvae were 13.0 mm; then the ratio declined to unity for larger larvae. In scaled sardine larvae (Houde 1977b), the ratio increased throughout the larval size range, but the relative increase in night catches was slight compared to thread herring.

Annual estimates of larval abundance by 1-mm length classes were calculated for 1971 and 1973 (Figure 10), after the data had been corrected for daytime avoidance. Abundance of larvae was slightly higher in 1973 than in 1971. The abundance of 3.0- to 7.0-mm larvae accounted for the difference between the two years (Figure 10). Larvae longer than 17.0 mm were more abundant in 1973 than in 1971.

Abundance of larvae decreased exponentially in both years as lengths increased (Figure 10). Exponential functions were fitted to data in the 4.1- to 19.0-mm length classes in 1971 and to the 5.1- to 20.0-mm length classes in 1973 (Figure 10), giving estimates of the instantaneous decline in abundance of thread herring larvae per millimeter increase in length. The instantaneous coefficients estimate larval mortality rates if gear avoidance

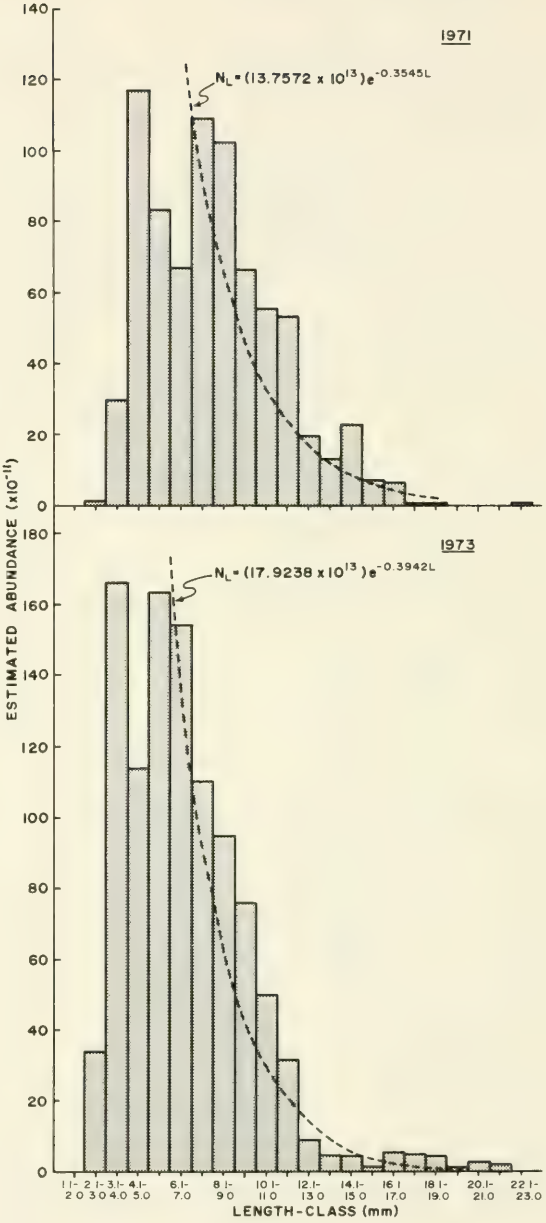

FIGURE 10.—Length–frequency distribution of annual larval abundance estimates for thread herring larvae collected in the eastern Gulf of Mexico, 1971 and 1973. Frequencies in each 1-mm length class are expressed as estimated annual abundance and have been corrected for daytime avoidance. Fitted exponential functions provide estimates of the instantaneous coefficient of decline in abundance by length.

is not too great over the length ranges in the analysis. Coefficients were $Z = 0.3545$ in 1971 and $Z = 0.3942$ in 1973. The corresponding percentage

losses per millimeter increase in length are 29.9% in 1971 and 32.6% in 1973. Confidence limits on Z at the 0.95 probability level were $Z \pm 0.0816$ in 1971 and $Z \pm 0.1385$ in 1973. The mortality coefficients did not differ significantly between years (t-test; $P>0.50$).

Mortality coefficients for round herring larvae per millimeter increase in length were $Z = 0.2269$ in 1971–72 and $Z = 0.3647$ in 1972–73 in the eastern Gulf of Mexico (Houde 1977a). Larval mortality of scaled sardines in 1973 was $Z = 0.3829$ (Houde 1977b), which is nearly identical to that for thread herring. Lenarz (1973) reported ranges of instantaneous coefficients for abundance at length data to be 0.15 to 0.33 for Pacific sardine, *Sardinops caeruleus,* and from 0.32 to 0.46 for northern anchovy, *Engraulis mordax,* larvae. The Pacific sardine coefficients were lower than those for thread herring, but the anchovy coefficients were similar to thread herring coefficients. Matsuura (in press) obtained a high instantaneous coefficient of $Z = 0.4962$ for Brazilian sardine, *Sardinella brasiliensis,* which is higher than any values observed for Gulf of Mexico clupeid larvae.

To obtain estimates of larval mortality relative to age rather than length, an exponential growth model was used to estimate age at length for thread herring larvae, given various mean daily growth increments during the larval stage. Mean daily growth increments of eastern Gulf clupeid larvae probably range from 0.3 to 1.0 mm based on laboratory rearing experiments for some species (Richards and Palko 1969; Saksena and Houde 1972; Saksena et al. 1972; Houde 1973b; Houde and Swanson 1975). At temperatures above 26°C, healthy larvae grew, on average, more than 0.5 mm/day. Duration of the egg stage for thread herring is about 0.84 days. The duration of nonfully vulnerable length classes also was estimated before mean age of each fully vulnerable 1-mm length class was calculated. Nonfully vulnerable length classes were 1.1 to 4.0 mm in 1971 and 1.1 to 5.0 mm in 1973. The duration of these stages in thread herring probably is from 1.0 to 3.0 days and 4.0 to 6.0 days, respectively, based on evidence from laboratory rearing of similar clupeid larvae (Houde et al. 1974; Houde and Swanson 1975). Eastern Gulf clupeid larvae quickly attain 4.0 mm length during the first day after hatching, but show no further growth in length until the fourth day after hatching. No direct observations of stage duration for thread herring larvae 5.0 mm or less in length were available from laboratory experiments but their growth pattern during this stage probably does not differ from that of other clupeids. Stage durations of nonfully vulnerable length classes were assigned based on observations of the other species. Methods and details of the mortality estimating procedure were given by Houde (1977a).

Two examples of duration-corrected abundance data assuming exponential growth of fully vulnerable larval length classes up to 19.0 mm in 1971 and 20.0 mm in 1973 are given in Table 7. In these examples, the mean daily growth increment was assumed to be 0.8 mm. Sets of such abundance

TABLE 7.—Two examples of data from 1971 and 1973 used to obtain stage duration, mean age, and duration-corrected abundance of thread herring eggs and larvae. Duration-corrected abundances were subsequently regressed on mean ages to obtain mortality rates (Table 8). Abundance estimates in the second column of the Table were previously corrected for daytime avoidance. In these examples, the mean daily growth increment ($\bar{b}$) was set at 0.80 mm. The nonfully vulnerable size classes were 1.1 to 4.0 mm in 1971 and 1.1 to 5.0 mm in 1973. Calculating procedures were given in Houde (1977a), Equations (12) to (16). Regressions for these data are presented in Figure 18.

Stage	Abundance (no. × 10^{11})	Duration (days)	Mean age (days)	Duration-corrected abundance (no. × 10^{11})	Stage	Abundance (no. × 10^{11})	Duration (days)	Mean age (days)	Duration-corrected abundance (no. × 10^{11})
		1971					1973		
Eggs	274.49	0.84	0.42	326.77	Eggs	921.24	0.84	0.42	1,105.93
1.1– 4.0 mm	31.65	1.00	1.34	31.65	1.1– 5.0 mm	313.69	4.00	2.84	78.42
4.1– 5.0	117.33	2.49	3.01	47.14	5.1– 6.0	163.32	2.04	5.79	80.13
5.1– 6.0	83.72	2.04	5.52	41.08	6.1– 7.0	154.18	1.73	7.88	89.33
6.1– 7.0	66.38	1.73	7.62	38.46	7.1– 8.0	109.80	1.50	9.68	73.35
7.1– 8.0	108.92	1.50	9.41	72.77	8.1– 9.0	94.93	1.32	11.25	71.84
8.1– 9.0	102.14	1.32	10.98	77.30	9.1–10.0	75.86	1.18	12.64	64.14
9.1–10.0	66.52	1.18	12.38	56.24	10.1–11.0	49.55	1.07	13.90	46.28
10.1–11.0	55.47	1.07	13.63	51.81	11.1–12.0	31.82	0.98	15.04	32.55
11.1–12.0	53.74	0.98	14.77	54.96	12.1–13.0	8.88	0.90	16.08	9.87
12.1–13.0	19.29	0.90	15.82	21.44	13.1–14.0	4.53	0.83	17.05	5.44
13.1–14.0	12.68	0.83	16.79	15.21	14.1–15.0	4.24	0.78	17.94	5.46
14.1–15.0	22.51	0.78	17.68	29.01	15.1–16.0	1.56	0.73	18.78	2.15
15.1–16.0	7.16	0.73	18.52	9.86	16.1–17.0	5.59	0.68	19.57	8.20
16.1–17.0	6.38	0.68	19.30	9.35	17.1–18.0	5.24	0.64	20.30	8.15
17.1–18.0	0.17	0.64	20.04	0.26	18.1–19.0	4.60	0.61	21.00	7.55
18.1–19.0	0.31	0.61	20.74	0.51	19.1–20.0	1.44	0.58	21.66	2.49

estimates, assigning other mean daily growth increments and other durations for nonfully vulnerable larvae, were generated. Duration-corrected abundances (Table 7) were then regressed on estimated mean ages, the resulting regression coefficients from the fitted exponential functions being estimates of the instantaneous mortality coefficients (Z) for age in days.

Examples of probable thread herring larval mortality estimates in 1971 and 1973 for a range of possible mean daily growth increments and for two probable stage durations of nonfully vulnerable larvae are given in Table 8. The ranges of probable larval mortality rates were similar in the two years. The probable instantaneous mortality coefficients ranged from 0.1371 to 0.2575 in 1971, corresponding to daily mortality rates of 12.8 to 22.7%. In 1973 the estimates of instantaneous mortality coefficients ranged from 0.1691 to 0.3050, which correspond to daily rates of 15.6 to 26.3%. The effect of varying the assumed duration of nonfully vulnerable stages had a relatively minor effect on mortality rate estimation compared with varying growth rates (Table 8).

The y-axis intercepts (N_0) of the exponential regressions used to obtain mortality estimates (Table 8) also estimate annual spawning by thread herring. The range of estimates in Table 8 encompasses the estimate obtained for 1971 and 1973 by the Sette and Ahlstrom (1948) or Simpson (1959) techniques (Tables 3, 4). At a mean daily growth increment of 0.8 mm, a probable value based on laboratory growth data, the annual spawning estimates from the y-axis intercepts (Table 8) are similar to those obtained by the other methods (Tables 3, 4).

I believe that the best estimates of larval mortality were generated from abundance and age data in Table 7. These data indicated that daily mortality of thread herring larvae was approximately 20% in both 1971 and 1973. Instantaneous mortality coefficients for conditions in Table 7 were $Z = 0.2124$ in 1971 and $Z = 0.2564$ in 1973, which correspond to daily mortality rates of 19.1 and 22.6% (Table 8). Regressions from which those instantaneous mortality coefficients were derived are given in Figure 11. Confidence intervals on Z at the 0.95 probability level ranged from 0.0990 to 0.3258 in 1971 and from 0.1993 to 0.3224 in 1973. The instantaneous coefficients were not tested to determine if they differed significantly between 1971 and 1973 because variances of the estimates were not homogeneous ($S_b^2 = 0.0028$ in 1971, $S_b^2 = 0.0007$ in 1973), but the overlapping confidence intervals indicated that they did not differ significantly.

Regressions of duration-corrected abundance on estimated mean age (Figure 11) suggested that

TABLE 8.—Summary of mortality estimates for thread herring larvae from the eastern Gulf of Mexico, 1971 and 1973. Estimates were obtained from the exponential regression of egg and larvae abundances on mean age. Instantaneous growth and mortality coefficients were calculated for various possible combinations of mean daily growth increment and duration of the nonfully vulnerable larval stages. Egg stage duration was assumed to be 0.84 days. Nonfully vulnerable larval stages were 1.1 to 4.0 mm SL in 1971 and 1.1 to 5.0 mm SL in 1973. Explanation of the estimating method is given in Equations (12) to (16) of Houde (1977a).

Year	Mean daily growth increment, $\bar{b}$ (mm)	Instantaneous growth coefficient, g	Nonfully vulnerable larvae duration (days)	Instantaneous mortality coefficient, Z	Y-axis intercept, N_0 (no. $\times 10^{11}$)	Daily mortality rate, $1 - \exp(-Z)$
1971	0.5	0.0498	1.0	0.1403	219.43	0.1309
	0.6	0.0598	1.0	0.1650	258.43	0.1521
	0.7	0.0698	1.0	0.1890	297.83	0.1722
	0.8	0.0797	1.0	0.2124	337.80	0.1913
	0.9	0.0897	1.0	0.2352	378.36	0.2096
	1.0	0.0997	1.0	0.2575	419.59	0.2270
	0.5	0.0498	3.0	0.1371	266.31	0.1281
	0.6	0.0598	3.0	0.1601	321.57	0.1479
	0.7	0.0698	3.0	0.1820	378.83	0.1664
	0.8	0.0797	3.0	0.2030	437.93	0.1837
	0.9	0.0897	3.0	0.2230	498.64	0.1999
	1.0	0.0997	3.0	0.2421	560.70	0.2150
1973	0.5	0.0498	4.0	0.1733	466.83	0.1591
	0.6	0.0598	4.0	0.2024	588.96	0.1832
	0.7	0.0698	4.0	0.2301	722.16	0.2056
	0.8	0.0797	4.0	0.2564	865.78	0.2262
	0.9	0.0897	4.0	0.2814	1,019.02	0.2453
	1.0	0.0997	4.0	0.3050	1,180.73	0.2629
	0.5	0.0498	6.0	0.1691	590.12	0.1556
	0.6	0.0598	6.0	0.1961	761.18	0.1780
	0.7	0.0698	6.0	0.2211	948.51	0.1983
	0.8	0.0797	6.0	0.2442	1,149.53	0.2167
	0.9	0.0897	6.0	0.2656	1,361.12	0.2333
	1.0	0.0997	6.0	0.2853	1,580.16	0.2482

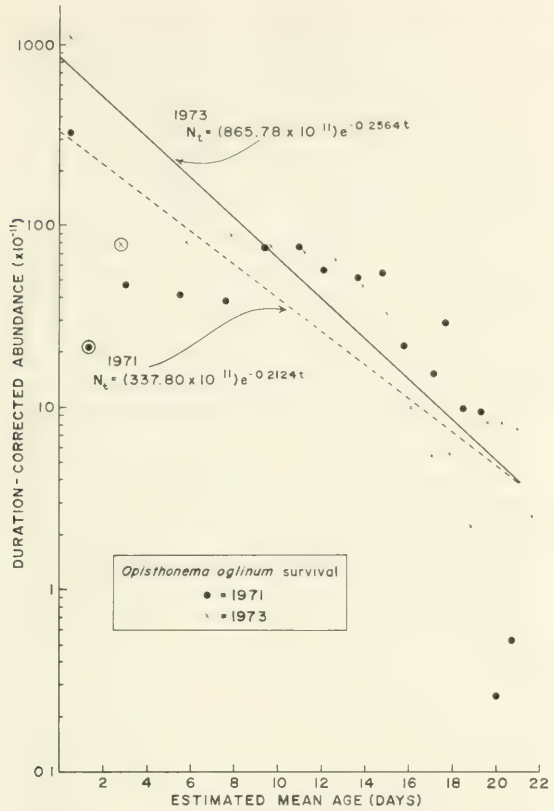

FIGURE 11.—Estimated abundance of egg and larval stages of thread herring in the eastern Gulf of Mexico in 1971 and 1973. Abundance is expressed as a function of estimated age. Fitted exponential functions give estimates of the instantaneous rates of decline in abundance for eggs and larvae up to 21 days of age. The two symbols enclosed in circles represent nonfully vulnerable length classes and were not included in the regression of instantaneous decline.

abundance of young larvae was underestimated in each year. If this is true, then mortality estimates (Table 8) are too low. Also, if growth was not exponential, but linear, then abundance of larvae in older age-classes was overestimated and mortality rates of thread herring larvae would be greater than estimates from the regression coefficients (Table 8).

Houde (1977a) estimated instantaneous mortality coefficients from abundance at age data for round herring larvae to be $Z = 0.1317$ in 1971–72 and $Z = 0.1286$ in 1972–73. These estimates are lower than the most probable rates for thread herring larvae. The estimated mortality coefficient ($Z = 0.2835$) for scaled sardine larvae in 1973 was similar to those for thread herring (Houde 1977b). The thread herring instantaneous mortality coefficients for abundance at age data were similar to those for Pacific sardine ($Z = 0.16$–0.17) (Ahlstrom 1954), jack mackerel ($Z = 0.23$) (Farris 1961), and Japanese mackerel ($Z = 0.3295$) (Watanabe 1970), but higher than those reported for Japanese sardine ($Z = 0.1279$) (Nakai and Hattori 1961) or plaice ($Z = 0.0209$ to 0.0685) (Bannister et al. 1974).

Estimated numbers and percentage survival of thread herring at hatching, 5.5 mm SL, and 15.5 mm SL were calculated given three possible instantaneous growth rates, corresponding to mean daily growth increments of 0.6, 0.8, and 1.0 mm (Table 9). The estimating procedure used parameters from the exponential functions describing decline in numbers by age (Table 8) and the age-at-length data assuming exponential growth (examples in Table 7). The estimated number of spawned eggs, from Table 3, varied by more than a factor of three between 1971 and 1973, yet the estimated number of survivors when larvae begin to transform to juveniles (15.5 mm SL) (Richards et al. 1974) was not much different between years (Table 9). Percentage survival from spawned egg to that stage did vary between 1971 and 1973; an estimated mortality of >99% occurred in 1973, but mortality was approximately

TABLE 9.—Estimated numbers and percentages of survivors of thread herring at hatching, 5.5 mm SL, and 15.5 mm SL in 1971 and 1973. Estimates are made at three possible growth rates (see Table 8). Duration of the nonfully vulnerable larval stages was set at 1.0 days for 1.1 to 4.0 mm larvae in 1971 and at 4.0 days for 1.1 to 5.0 mm larvae in 1973. The number of spawned eggs in each year was based on the estimates in Table 3. Predicted numbers at hatching, 5.5 mm, and 15.5 mm are calculated from exponential functions based on Table 8 data.

Year	Instantaneous growth coefficient, g	Number of spawned eggs ($\times 10^{11}$)	Instantaneous mortality coefficient, Z	Number hatching ($\times 10^{11}$)	Percent mortality[1] to hatching	Number of 5.5-mm larvae ($\times 10^{11}$)	Percent mortality to 5.5 mm	Number of 15.5-mm larvae ($\times 10^{11}$)	Percent mortality to 15.5 mm
1971	0.0598	326.77	0.1650	224.98	31.2	84.85	74.0	4.86	98.5
	0.0797	326.77	0.2124	282.60	13.5	104.59	68.0	6.61	98.0
	0.0997	326.77	0.2575	337.98	—	122.22	62.6	8.42	97.4
1973	0.0598	1,105.93	0.2024	496.88	55.1	171.35	84.5	5.14	99.5
	0.0797	1,105.93	0.2564	698.02	36.9	196.19	82.3	7.02	99.4
	0.0997	1,105.93	0.3050	913.87	17.4	213.98	80.7	9.00	99.2

[1]Hatching assumed to occur at 0.84 days.

98% in 1971. Estimated percentage mortalities from spawning to hatching (Table 9) were lower for thread herring than those estimated previously for round herring (35 to 90%) from the eastern Gulf (Houde 1977a). They also were lower than those (>85%) estimated for scaled sardines (Houde 1977a) in 1973. The 5.5 mm SL stage represents postyolk-sac thread herring larvae that had succeeded in starting to feed; percentage mortality to that stage was estimated to range from 62.6 to 84.5% (Table 9).

The 15.5-mm stage would be attained at 18.5 to 19.0 days if the instantaneous growth coefficient was 0.0797 (equals 0.80-mm mean daily growth increment) (Table 7). At that growth rate 20 larvae/1,000 spawned eggs would have survived to 15.5 mm SL in 1971, but only 6 larvae/1,000 eggs would have survived to 15.5 mm in 1973 (Table 9). The expected number of thread herring survivors at 15.5 mm/1,000 spawned eggs was similar to that estimated for round herring from the eastern Gulf (Houde 1977a), but greater than the number estimated for scaled sardines (Houde 1977b).

SUMMARY

1. Spawning by thread herring in the eastern Gulf of Mexico occurred from February to September, based on catches of larvae from March through September and eggs from May through August. Most spawning took place from April to August in depths <30m, within 50 km of the coast. Spawning was most intense between lat. 26°00′N and 28°00′N (Fort Myers to Tampa Bay, Fla.).

2. Eggs were collected when surface temperatures ranged from 22.5° to 30.3°C and when surface salinities were 32.4 to 36.8‰. Larvae ≤5.0 mm SL were collected at surface temperatures from 18.5° to 30.9°C and at surface salinities from 27.3 to 36.9‰. Most eggs and ≤5.0-mm larvae were taken when surface temperature exceeded 25°C and when surface salinity was above 35.0‰.

3. Estimates of adult biomass ranged from 108,000 to 372,000 metric tons in 1971 and 1973. The 0.95 confidence intervals on 1971 and 1973 estimates range from 72,800 to 428,800 metric tons.

4. The estimated concentration of adult thread herring biomass from the coast to the 50-m depth contour was in the range of 6.8 to 40.2 kg/ha. The total area in which thread herring occurred was 106.7×10^5 ha.

5. Estimates of annual potential yield to a fishery, based on 1971 and 1973 biomass estimates, ranged from 27,500 to 186,200 metric tons of adult thread herring. The potential yield, based on the mean of 1971 and 1973 biomass estimates, was between 60,300 and 120,600 metric tons.

6. Larval abundance was greater in 1973 than in 1971. Mortality rates for larval thread herring were estimated by length and for estimated ages. For lengths, the instantaneous coefficients of decline in catches were $Z = 0.3545$ in 1971 and $Z = 0.3942$ in 1973, corresponding to 29.9 and 32.6% losses per millimeter of growth. For age, the most probable daily mortality estimates were $Z = 0.2124$ in 1971 and $Z = 0.2564$ in 1973, which correspond to daily loss rates of 19.1 and 22.6%.

7. It is probable that >99% mortality occurred between spawning and the 15.5-mm stage in 1973, and that approximately 98% mortality occurred in 1971. About 20 larvae/1,000 spawned eggs were estimated to have survived to 18.5 to 19.0 days after hatching and 15.5 mm SL in 1971, but only 6 larvae/1,000 eggs were estimated to have survived to that stage in 1973.

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CHLORINATED HYDROCARBONS IN DOVER SOLE, *MICROSTOMUS PACIFICUS*: LOCAL MIGRATIONS AND FIN EROSION

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ABSTRACT

Dover sole, *Microstomus pacificus*, with and without fin erosion were collected from the municipal wastewater discharge sites of Los Angeles and Orange counties. While there was a significant difference between the total DDT levels in muscle tissue of the unaffected fish from the two regions, there was no significant regional difference between the muscle DDT levels in the diseased fish. This is consistent with the proposed hypothesis that the Orange County diseased fish had originated at the Los Angeles County discharge site. Comparisons of chlorinated hydrocarbon levels in diseased and unaffected Dover sole from the Palos Verdes discharge site of Los Angeles County indicate: 1) DDT levels were significantly higher ($P<0.05$) in Dover sole with fin erosion, and 2) polychlorinated biphenyl levels were higher at the 90% confidence level ($P<0.10$) in diseased Dover sole.

In recent years, fin erosion diseases have been observed in several species of marine fishes collected from areas contaminated by industrial or municipal waste such as the Duwamish River estuary, Wash. (Wellings et al. 1976), the New York Bight (Mahoney et al. 1973; Murchelano 1975), and major municipal wastewater discharge sites in the Southern California Bight (Mearns and Sherwood 1974). In southern California, the disease is most prevalent in the Dover sole, *Microstomus pacificus* Lockington, a marine flatfish.

Dover sole with fin erosion occur most frequently near the Palos Verdes discharge site of the Joint Water Pollution Control Plant (JWPCP) submarine outfalls of the County Sanitation Districts of Los Angeles County. During the period 1972–76, 39% of the 20,854 Dover sole collected in 268 samples off Palos Verdes had fin erosion. Only 3.5% of 894 individuals collected in Santa Monica Bay to the north (109 samples), 2.0% of 5,354 individuals collected in south San Pedro Bay to the south (138 samples), and 0.67% of 889 individuals collected off Dana Point farther south (77 samples) were affected with the disease.

The JWPCP outfalls are the dominant source of DDT residues (total DDT) and most trace metals introduced via municipal wastewaters to the Southern California Bight (Galloway 1972; Young et al. 1973; Young et al. 1976b). Although in 1974 Orange County's discharge of polychlorinated biphenyl (PCB) was twice that of any other discharger (Young et al. 1976a), the sediments off the Palos Verdes Peninsula, as a result of past discharges, have the highest levels of total PCB and total DDT found in marine sediments of the Bight (Young et al. 1976a, b).

The Dover sole is one of the most abundant and most frequently encountered species in trawl catches taken in the vicinity of the southern California submarine municipal wastewater outfalls (Southern California Coastal Water Research Project 1973). In southern California, as in northern California where it is the focus of a major bottom fishery (Hagerman 1952), Dover sole undergo seasonal onshore–offshore migrations (Mearns and Sherwood 1974). Individuals move offshore in the winter and onshore in the summer and have been collected off southern California at depths generally greater than 25 m.

In May and August 1972, trawl catches taken in the vicinity of the Orange County outfall system in south San Pedro Bay contained higher numbers of Dover sole with fin erosion than did previous catches (6 of 684 individuals and 34 of 611 individuals, respectively). This increase was associated with a large influx of Dover sole into the area. Only 273 individuals had been collected in February 1972. Orange County trawls were taken at a standard set of eight stations with the same gear and vessel combination. Only larger individuals (generally >120 mm standard length, SL) were affected with the disease; this contrasted with the situation off Palos Verdes, where Dover

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sole <120 mm SL also had eroded fins. These observations suggested that Dover sole with fin erosion caught in the vicinity of the Orange County outfall could have migrated from the Palos Verdes shelf (Mearns and Sherwood 1974). Since the increase had occurred 13 mo after the depth of discharge off Orange County had been changed from 20 to 60 m, within the range of the Dover sole, one objective of this study was to test the hypothesis that the diseased fish collected off Orange County had migrated from the Palos Verdes region and that the disease did not originate in the Orange County area. Since collections on the Palos Verdes shelf contained the highest percentage of Dover sole with fin erosion and the shelf was also the site of highest bottom sediment contamination by total DDT, we attempted to use this contamination as a tag of exposure to the JWPCP discharge area. Reported values for the biological half-life of DDT compounds in fish generally range from about 1 to 5 mo (Buhler et al. 1969; Grzenda et al. 1970; Hansen and Wilson 1970; Macek et al. 1970). Since the Orange County discharge site is about 35 km to the south of the JWPCP discharge area, it is possible that movement over this distance could occur before a significant fraction of the accumulated DDT residues had been depleted.

In Dover sole, external signs of the disease were restricted to the fins. The noninflammatory nature of the lesions and the absence of any demonstrable organisms associated with the lesions, as determined by histological examination, suggest that the disease is not the result of an infectious process (Klontz and Bendele[3]). If chemical agents are involved, then it is possible that concentrations of these agents in tissues might reflect their involvement in disease development. A second objective of this study was to explore the role of chlorinated hydrocarbons in the fin erosion disease by determining if there were differences between the levels of total DDT and total PCB in muscle tissue of Dover sole with and without eroded fins.

SAMPLING AND ANALYSIS

Fish analyzed in this study were subsamples of collections made during routine trawl monitoring surveys by the County Sanitation Districts of Los Angeles and Orange counties. During 1974, up to four trawl series were conducted off the Palos Verdes Peninsula and Orange County (Figure 1). The trawls off Orange County were conducted with a Marinovich semiballoon otter trawl with a 7.6-m (25-ft) headrope and a 1.3-cm (0.5-in) stretch mesh cod end liner. Hauls off Palos Verdes were made with a net of identical dimensions but of heavier construction and otter boards.[4] The nets were towed at a speed of 1.3 m/s (2.5 knots) and remained in contact with the ocean floor for 10 min. When the net was brought aboard ship, specimens of Dover sole, with eroded fins (diseased) and without eroded fins (unaffected), were removed, bagged, labeled, and immediately frozen. The frozen samples were returned to the laboratory and placed in freezers.

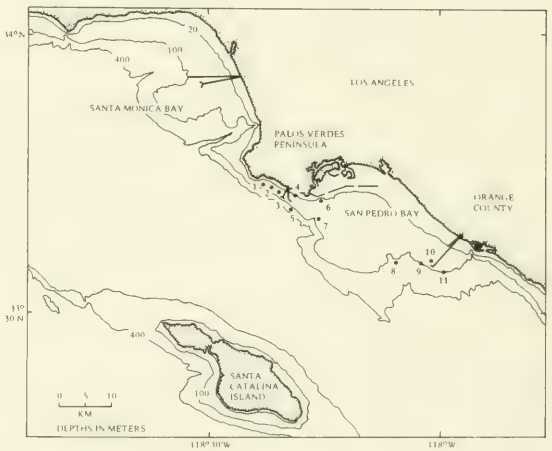

FIGURE 1.—Stations off Palos Verdes and Orange County at which Dover sole were collected.

The following numbers of Dover sole were obtained from each of the 1974 quarterly trawl series: winter (December 1973–February 1974), 10 from off Palos Verdes; spring (March–May 1974), 15 from off Palos Verdes and 5 from off Orange County; summer (June–August 1974), 6 from off Palos Verdes; and fall (September–November 1974), 17 from off Orange County.

The mean and the standard error of the standard lengths for the Palos Verdes samples with (n = 16) and without (n = 15) eroded fins were

[3]Klontz, G. W., and R. A. Bendele. 1973. Histopathological analysis of fin erosion in southern California marine fishes. South. Calif. Coastal Water Res. Proj., Rep. TM 203.

[4]This net was constructed for the Coastal Water Project by J. Willis, Morro Bay, Calif.

174 ± 3 mm and 193 ± 6 mm, respectively; the respective body weights were 78 ± 5 g and 115 ± 11 g. Measurements for the diseased (n = 14) and unaffected (n = 8) Orange County specimens were 195 ± 4 mm and 182 ± 7 mm SL, 119 ± 8 g and 98 ± 10 g, respectively. These fish were generally 3 to 4 yr old, though some were younger and some older. The mean standard lengths of several age-classes of over 425 southern California Dover sole collected at coastal locations by small otter trawl were as follows: age-class I, 70 mm; II, 140 mm; III, 170 mm; IV, 190 mm; V, 220 mm (Mearns and Harris[5]).

Muscle tissue subsamples were excised from each of the specimens when they were semi-thawed. The dissections were performed on cleaned Teflon[6] sheets, using carbon steel implements. The tissue samples were placed in glass containers, which had been heated overnight in a kiln at 538°C (1,000°F). The samples were then frozen until chemical analyses were performed.

Levels of total DDT and total PCB were measured in the samples using electron-capture gas chromatography (Young et al. 1976b). The components were identified by retention time; values were derived by comparing the peak heights of the samples with the peak heights of standards.

RESULTS AND DISCUSSION

Migration Hypothesis

The hypothesis that the diseased Dover sole collected off Orange County had migrated from the Palos Verdes shelf was tested by measuring the levels of total DDT and total PCB in muscle tissue from specimens with and without eroded fin tips from both locations. To discount possible seasonal variability, all results obtained for each disease category at an individual station were combined on a quarterly basis. To discount possible station variability, only data from those stations for which both diseased and unaffected specimens had been analyzed were used. For comparison, we used the median total DDT and total PCB concentrations for diseased and unaffected fish. Tables 1 and 2 present the results for total DDT and total PCB, respectively.

TABLE 1.—Median concentrations (milligrams per kilogram wet weight) of total DDT in muscle tissue of Dover sole, with and without eroded fins, collected off Palos Verdes Peninsula and Orange County, 1974 quarterly trawl series.

Location Station	Quarter	Diseased (with eroded fins) n	Median	Range	Unaffected (without eroded fins) n	Median	Range
Palos Verdes:							
5	Winter	3	18	15 –29	2	7.0	2.0–12
7	Winter	2	36	29 –44	3	1.8	1.3– 2.3
1	Spring	2	26	18 –34	1	25	—
2	Spring	2	20	16 –24	3	5.0	4.3– 5.3
3	Spring	3	13	7.2–45	2	11	9.6–13
4	Spring	1	16	—	1	14	—
6	Summer	3	15	8.0–29	3	11	8.8–13
Orange County:							
8	Spring	4	31	19 –75	1	7.6	—
10	Fall	6	7.6	4.2–57	2	1.0	0.3– 1.7
11	Fall	1	19	—	2	1.2	0.3– 2.2
9	Fall	3	4.2	0.9– 6.1	3	0.4	0.4– 0.5

TABLE 2.—Median concentrations (milligrams per kilogram wet weight) of total PCB in muscle tissue of Dover sole, with and without eroded fins, collected off Palos Verdes Peninsula and Orange County, 1974 quarterly trawl series.

Location Station	Quarter	Diseased (with eroded fins) n	Median	Range	Unaffected (without eroded fins) n	Median	Range
Palos Verdes:							
5	Winter	3	2.6	1.8–3.6	2	1.2	0.6–1.9
7	Winter	2	3.8	3.4–4.3	3	0.3	0.2–0.5
1	Spring	2	2.0	1.7–2.2	1	2.6	—
2	Spring	2	2.4	1.5–3.4	3	0.5	0.4–0.6
3	Spring	3	1.0	0.8–3.0	2	1.4	1.4–1.5
4	Spring	1	2.1	—	1	1.6	—
6	Summer	3	1.5	0.6–3.3	3	1.0	0.8–2.6
Orange County:							
8	Spring	4	3.0	2.1–6.6	1	0.9	—
10	Fall	6	3.4	1.3–5.2	2	4.0	1.8–6.2
11	Fall	1	1.6	—	2	0.3	0.3
9	Fall	3	0.9	0.9–1.1	3	0.3	0.2–0.3

Using the Mann–Whitney U-test, we found no significant difference ($P>0.20$) between total DDT concentrations in the muscle tissue of diseased fish from the Orange County and Palos Verdes regions. The overall median total DDT concentrations were 13 and 18 mg/kg wet weight, respectively. In contrast, there was a significant difference ($P<0.05$) between total DDT levels in the unaffected fish from the two regions (overall medians of 1.1 and 11 mg/kg wet weight, respectively).

In this study, the overall median values obtained for total DDT levels in diseased Dover sole from both areas and in the unaffected fish from Palos Verdes were 10 or more times greater than the overall median value obtained for the unaffected Orange County specimens. McDermott and Heesen (1975) had previously found that the

[5]Mearns, A. J., and L. H. Harris. 1975. Age, length, and weight relationships in southern California populations of Dover sole. South. Calif. Coastal Water Res. Proj., Rep. TM 219.

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

median level of total DDT in muscle tissue from Dover sole collected off Palos Verdes was about 10 times greater than the median level observed for the Orange County specimens (McDermott and Heesen[7]).

These results support the hypothesis that the Dover sole with fin erosion collected off Orange County came from the Palos Verdes population. They also suggest that levels of DDT in tissues may be used as a tag when investigating local migrations of fish from or across a known point source of DDT.

There were no significant differences ($P>0.20$) between the total PCB levels in unaffected Dover sole from Orange County and Palos Verdes, nor between the total PCB levels in diseased fish from the two areas. The overall median total PCB concentrations in muscle tissue of unaffected fish from Orange County and Palos Verdes were 0.6 and 1.2 mg/kg wet weight, respectively; from diseased specimens, 2.3 and 2.1 mg/kg wet weight, respectively.

Association of Chlorinated Hydrocarbons with Fin Erosion

Since the diseased fish at Orange County appear to have originated from Palos Verdes and the Palos Verdes area is the primary site of total DDT and total PCB sediment contamination, only the results obtained for total chlorinated hydrocarbon measurements in diseased and unaffected Dover sole collected from Palos Verdes were utilized to test for the association of chlorinated hydrocarbons with fin erosion. Using the Mann–Whitney U-test we found that the DDT levels in diseased Palos Verdes Dover sole were significantly greater ($P<0.05$) than the DDT levels measured in unaffected Palos Verdes specimens. The overall median values for diseased and unaffected Dover sole were 18 and 11 mg/kg wet weight, respectively.

Differences in the levels of total PCB in the muscle tissue of diseased and unaffected Dover sole were significant only at the 90% confidence level ($P<0.10$). Thus there was a tendency for the total PCB levels to be higher in the diseased fish. The median values for the diseased and unaffected groups were 2.1 and 1.2 mg/kg wet weight, respectively.

These results indicate that there is a significant association between high levels of total DDT and fin erosion, and a possible association between high levels of total PCB and fin erosion in Dover sole collected off Palos Verdes.

There are several possible reasons for these associations. DDT and PCB in combination with each other and/or other constituents present in this region (such as hydrogen sulfide, high levels of trace metals, or abrasive materials) could be involved in the development of the disease. Alternatively, chlorinated hydrocarbon uptake could be enhanced in diseased fish; hence the higher levels might be the result of the disease rather than a cause. A third possibility is that the fish with fin erosion have been present on the Palos Verdes shelf longer than the unaffected fish and have been exposed to the chlorinated hydrocarbons for a longer period of time. These possible explanations are presently under investigation.

It is interesting to note that while the Palos Verdes municipal wastewater discharges of DDT significantly decreased from greater than 20 metric tons in 1971 to 2 metric tons in 1974 (Young et al. 1975), the levels of DDT in the Dover sole have remained unchanged (McDermott and Heesen see footnote 7). Similarly, the level of DDT in the surface sediments off the Palos Verdes Peninsula remained relatively constant over the 3-yr period, 1971–73 (Young et al. 1975; Young et al. 1976b). The situation for PCB is similar. The discharge of PCB decreased from greater than 19 metric tons in 1972 to 5 metric tons in 1974 (Young et al. 1976a) and the levels of PCB in the Dover sole remained unchanged (McDermott et al. 1976). Unfortunately, reliable historical data for PCB's in the Palos Verdes surface sediments are not available. The overall prevalence of fin erosion in Dover sole also remained relatively constant over the same time period (Sherwood and Mearns[8]). These findings point to the potentially significant role that the sediments may have in the uptake of chlorinated hydrocarbons and in the development of fin erosion in Dover sole.

[7]McDermott, D. J., and T. C. Heesen. 1975. DDT and PCB in Dover sole around outfalls. *In* Coastal water research project annual report, p. 117–121. South. Calif. Coastal Water Res. Proj., El Segundo.

[8]Sherwood, M. J., and A. J. Mearns. 1975. Sampling diseased fish populations. *In* Coastal water research project annual report, p. 27–32. South. Calif. Coastal Water Res. Proj., El Segundo.

SUMMARY

1. Levels of DDT in Dover sole with fin erosion collected off Palos Verdes and Orange County were not significantly different. This is consistent with the hypothesis that the Orange County diseased fish migrated from the Palos Verdes region and that the disease did not originate at Orange County.
2. A dominant point source discharge of a contaminant, such as the municipal wastewater discharge of DDT compounds off Palos Verdes, may provide a useful tag when investigating the migration of fish from or across that point source.
3. Dover sole with fin erosion from Palos Verdes have significantly higher levels of total DDT ($P<0.05$) than Dover sole without the disease from the same region.
4. There is a tendency for Dover sole with fin erosion from Palos Verdes to have higher levels of PCB ($P<0.10$) than Dover sole without the disease from the same region.

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DIEL BEHAVIOR OF THE BLUE SHARK, *PRIONACE GLAUCA*, NEAR SANTA CATALINA ISLAND, CALIFORNIA[1]

TERRY C. SCIARROTTA[2] AND DONALD R. NELSON[3]

ABSTRACT

The diel activity levels and movements of the blue shark, *Prionace glauca*, were studied in the natural environment using ultrasonic telemetry. Two initial sharks were tagged with single-channel transmitters equipped with depth sensors. Twelve sharks were tagged with multichannel transmitters with various combinations of sensors to measure depth, swimming speed, swimming direction, and temperature. From March to early June, the sharks made an evening-twilight migration from their epipelagic daytime habitat to the shallower waters bordering the island. From late June to October, the sharks remained offshore throughout the day and night. This change in movement pattern is suggested to be in response to a seasonal shift in location of prey. The telemetry data indicated that the blue shark is basically nocturnal, showing highest activity in the early evening and lowest activity in the early daylight morning. Measured parameters increasing at night included 1) rate of horizontal movement, 2) swimming speed, 3) variability in depth, and 4) variability in swimming direction. The sharks usually remained within a relatively narrow range of water temperatures.

This paper describes a study in which the diel activities of an epipelagic shark were monitored remotely in the natural environment. Multichannel ultrasonic transmitters were used to telemeter certain behavioral and environmental parameters of free-ranging blue sharks, *Prionace glauca* (Linnaeus). The primary objective was to track the sharks continuously throughout the day-night cycle to determine diel patterns of activity and movement.

Prior to the initiation of this study, surprisingly little had been published on the behavior of the blue shark, one of the most abundant large predators in warm temperate seas. Bigelow and Schroeder (1948) summarized what was then known about the biology of the species. Suda (1953) studied embryonic development, size relationsips, and sex ratios as related to distribution in the north tropical and subtropical Pacific. Strasburg (1958) investigated the distribution, abundance, capture depths, reproduction, and food habits of pelagic sharks, including the blue shark, in the central Pacific. Miscellaneous data on blue sharks have been reported from the Atlantic (Aasen 1966), the Canadian Atlantic (Templeman 1963), and the Gulf of Alaska (LeBrasseur 1964). A study of the blue shark off southern California, still largely unpublished, was conducted by Bane (1968).

More recently, the blue sharks off southwest England have received investigation in regard to age determination, reproduction, diet, and migration (Stevens 1973, 1974, 1975, 1976; Clarke and Stevens 1974). Casey, Stillwell, and Pratt at Narragansett, R.I. have gathered considerable information on the biology of sharks of that area, including data on migrations, food habits, and reproduction of blue sharks (Weeks 1974; Casey 1976; Stevens 1976). Tag returns from these studies have documented some long-range, long-term movements by blue sharks in the Atlantic. Several similar movements have also occurred in the Pacific (Bane 1968; D. R. Nelson, unpubl. data—see Discussion). Short-term movements, however, such as related to the diel cycle, have not been described for the blue shark.

Observations relating to the diel patterns of sharks have been mentioned by several authors (Springer 1963; Limbaugh 1963; Randall 1967; Hobson 1968), but specific quantitative studies have been few. Nelson and Johnson (1970) found that the horn shark, *Heterodontus francisci*, and the swell shark, *Cephaloscyllium ventriosum*, exhibited distinctly nocturnal activity patterns

[1]Adapted in part from the Masters Thesis of the senior author, Sciarrotta.

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under laboratory and field conditions. In subsequent work with the horn shark, Finstad and Nelson (1975) measured the effect of light intensity on releasing activity onset, both in the natural environment and in the laboratory under artificial twilight transitions. For a colony of captive bonnethead shark, *Sphyrna tiburo,* under semi-natural conditions, Myrberg and Gruber (1974) reported a late-afternoon peak in patrolling speed, suggesting a diurnal activity rhythm.

Using ultrasonic telemetry, Standora (1972) established a basically nocturnal pattern of activity and a limited home range for the Pacific angel shark, *Squatina californica.* His multichannel transmitters were a similar, but earlier version of those used in the present study. Carey and Lawson (1973) tracked a free-ranging dusky shark, *Carcharhinus obscurus,* in order to study body temperature regulation. They used a two-channel, frequency-shifting transmitter that measured both surface and deep body temperatures. Thorson (1971) monitored long-term movements of the bull shark, *C. leucas,* with relatively long-life, sensorless pingers and automatic-recording receivers at several locations. Using this technique in conjunction with conventional tagging, he showed that bull sharks move via the San Juan River from the Caribbean Sea to Lake Nicaragua.

The present paucity of behavioral information on active, wide-ranging sharks, especially pelagic species, is undoubtedly due in part to the difficulty of studying them by direct observation. Ultrasonic telemetry now offers one promising avenue of approach to this problem. This paper reports on an initial study using this technique to investigate diel patterns of behavior in a wide-ranging pelagic shark.

METHODS

The present study is based on 14 individual telemetry trackings conducted between 3 March and 7 October 1972 (Table 1). Each tracking was initiated in the pelagic environment of the San Pedro Channel approximately 6 to 7 km north of the Isthmus, Santa Catalina Island, Calif. The blue shark was well suited for this telemetry study because of its moderately large size, high abundance for most of the year, and attractability to bait. The abundance and/or attractability of blue sharks in the offshore baiting area was low only during the months of January and February, the sharks being easily obtainable the rest of the year.

TABLE 1.—Summary of tracking data for 14 telemetered blue sharks.

Tracking no.	Date (1972)	Estimated TL (m)	Sex	Tracking duration (h)	Tracking period	Evening shoreward movement
1	3/3	1.8	M	7.0	1040–1740	?
2	3/11	2.3	F	8.5	0910–1740	?
3	3/17	2.3	?	6.4	1105–1730	beginning
4	3/30	2.0	M	11.6	1125–2300	yes
5	4/7	2.6	M	8.4	1145–2010	yes
6	4/15	2.0	F	16.1	1155–0400	yes
7	4/29	1.8	F	18.0	1200–0600	yes
8	5/6	2.0	M	21.9	1010–0805	yes
9	5/20	2.0	F	19.6	1155–0730	yes
10	6/3	2.2	M	16.3	1615–0830	yes
11	6/14	2.3	M	4.8	1145–1630	?
12	6/24	2.3	M	14.8	1445–0530	no
13	9/13	2.0	F	13.4	1305–0230	no
14	10/7	2.0	F	18.8	1215–0700	no

The estimated range in total lengths of blue sharks telemetered was 1.8 to 2.6 m; for those otherwise observed, 1.2 to 3.0 m.

Telemetry System

The ultrasonic telemetry system used in the present study has been described in detail by Standora (1972), Ferrel et al. (1974), and Nelson (1974). The transmitters were of the oil-filled type, about 15 to 18 cm long, 3.5 cm in diameter, and emitted 10-ms pulses (tone bursts) at 40 kHz. The units were set for a life of several days, and a maximum range of 3 km (average conditions) to 5 km (ideal conditions). Data were encoded as pulse rate (pulse interval) which varied with the value of resistive sensors. The first two trackings utilized single-channel transmitters incorporating depth sensors. The remaining 12 trackings were performed with multichannel units (rapid-multiplexing type) with various combinations of sensors to measure depth, swimming speed, swimming direction, and temperature.

Two commercial tunable ultrasonic receivers were used. For continuous monitoring of relatively clear, nearby signals, the Smith–Root Ta-25[4] receiver (25–80 kHz) was employed using an omnidirectional hydrophone on a 25-m cable. The more sensitive, narrow-band DuKane model N15A235 receiver (30–45 kHz) with its staff-mounted directional hydrophone was used for directional tracking and for reception of weaker signals.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Application, Tracking, and Recovery

The sharks to be tagged were attracted with bait to the 7-m tracking boat. Cut Pacific mackerel, *Scomber japonicus,* in two bait cannisters, was suspended at depths of about 5 and 15 m. Since drifting of the boat established the odor corridor necessary for shark attraction, the time needed for attraction decreased as the wind (and drift rate) increased. The time necessary to attract the first blue shark ranged from 10 min to 4 h and the mean was 1.5 h.

Whenever a choice was possible, a larger individual shark was selected for tagging in order to lessen the possible effect of the transmitter on its behavior. The shark to be tagged was enticed to the surface next to the boat using a short baited line, then harpoon tagged in the middorsal region anterior to the first dorsal fin. The sex of the shark was noted and its total length estimated (Table 1). An attempt was made to prevent the shark from actually taking the bait, as this might have influenced subsequent feeding motivation.

The transmitter was attached to the shark by a stainless steel dart (Floy FH 69) thrust beneath the skin with a hand-held applicator pole. The transmitter package included a syntactic foam float and a magnesium breakaway link which corroded through in a roughly predictable time, allowing the unit to float to the surface for recovery.

The tracking procedure involved continuous monitoring of the signal from the drifting boat using the omnidirectional hydrophone. As the signal became weak, its direction was determined with the directional hydrophone, and the boat was then moved closer to the shark. Distance to the shark was estimated primarily from approximate signal strength and by triangulation from successive positions of the moving boat. To minimize the effect of the boat on the shark's behavior, an effort was made to maintain a distance of at least 200 m between the boat and the shark.

Ultrasonic tracking in the study area at times presented certain problems. Noise from crustaceans, echo-locating cetaceans, ship traffic, wave action, hydrophone turbulence, and bottom echoes could be picked up by the receivers, and if of high enough level, would mask the data pulses. Signal reception was also affected when the shark went below the thermocline (reflection) or was swimming very near the surface (wave shielding, bubble attenuation, downward ray refraction). These factors at times caused signal losses that could be counteracted only by lowering the hydrophone to a depth of about 10 or 15 m.

Data Recording and Reduction

Approximately once per half-hour, a 30-s data sequence was recorded on magnetic tape and the estimated position of the shark plotted. The omnidirectional hydrophone was preferred for recording purposes whenever the signal was sufficiently strong. It was less convenient to use the directional hydrophone for recording long data sequences because of the difficulty of maintaining continuous accurate aim, thus resulting in greater signal-strength variability.

Decoding of the single-channel depth data required only a stopwatch and calibration graph. Ten pulse intervals were timed and converted to a depth value. For the multichannel data, the tape recordings were converted into paper oscillograms on which the pulse intervals were measured manually. For analysis, the mean value for three clear 8-channel sequences were graphed for each half-hour recording period.

RESULTS

The telemetered blue sharks were generally most active at night, with highest activity in the early evening and lowest activity in the early daylight morning. While some activity occurred throughout the diel cycle, the mean recorded values for all trackings were greater at night for 1) rate of horizontal movement, 2) swimming speed, 3) variability in depth, and 4) variability in swimming direction. Experienced tracking personnel were also able to detect by ear subtle changes in the multiplexed pulse intervals. Although not quantified, the trackers received the distinct impression that these changes occurred more often at night—thus further supporting a nocturnal activity maximum.

Horizontal Movement—Island-Oriented Migration

The most striking behavior demonstrated by the present study was a seasonal, evening-twilight migration from the epipelagic offshore habitat to the shallower waters bordering the island. Between late March and early June, each of the seven sharks tracked made this movement to-

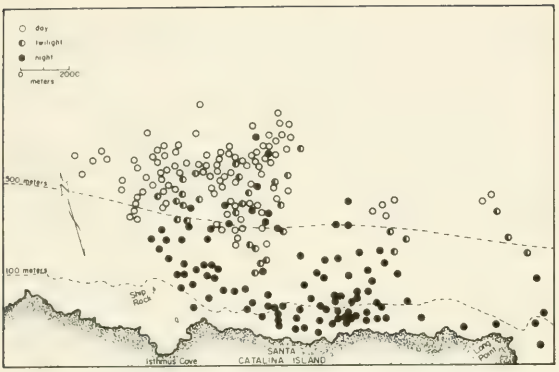

FIGURE 1.—Positions of seven blue sharks tracked from late March through early June 1972. Note that all day positions are offshore from the island, while the majority of night positions are nearshore, often in relatively shallow water.

wards the island shoreline. Examples of trackings of this type are shown in Figures 1 and 2.

These sharks remained offshore in the general vicinity of the tagging during the daylight hours. Approximately at dusk, the sharks initiated a relatively straight-line course towards the island. It is difficult to place precise times on when the sharks began this move, but it appeared to be from about 1.6 h before to 1.3 h after sunset, with a mean slightly after sunset. During the shoreward movement, the sharks swam at depths varying from near the surface to over 90 m. Once near the island, the sharks usually moved in an easterly direction parallel to the shoreline. Several hours before sunrise, there was a directed movement away from the island back to the offshore environment. The closest estimated nighttime approaches to the island for these individuals averaged 1,100 m (range, 200–4,000), corresponding to water depth averaging 115 m (range, 80–380).

Although three preliminary trackings in early and mid-March ended prior to nightfall, the last of these appeared to show the beginnings of a shoreward movement prior to transmitter release. One tracking in mid-June ended prematurely prior to dusk. From late June until early October, the three sharks successfully tracked remained offshore throughout the day and night over bottom depths of 500 m or more (Figures 3, 4).

Rate of Horizontal Movement

Rate of movement was calculated for each shark from its half-hourly estimated positions such as shown in Figures 2 and 4. The mean values for all sharks tracked (Figure 5) showed an increase in rate of movement at sunset which continued through most of the night. The mean rate of movement for the daytime was 1.2 km/h (range, 0.3–7.0); for the nighttime, 1.8 km/h (range, 0.4–4.0).

Swimming Speed

There was a definite increase in telemetered instantaneous swimming speed at night (Figure 5). However, no abrupt increase in speed occurred at the dusk transition, as might be expected in view of the rate of movement increase at that time. Swimming speed peaked a few hours after sunset and remained comparatively high until a few hours before sunrise. The artifactual burst of speed immediately after tag application was short lived, even in those sharks that did not promptly return to the bait cannister.

Although the maximum speed capability of the sensor was 5 km/h, this speed was not often reached during the half-hourly data recording periods, which suggests speeds in excess of 5 km/h seldom occurred. The mean swimming speed for the daytime was 1.3 km/h, for the nighttime 2.8 km/h, while the range for both covered the entire sensor range.

Increases in swimming speed were often associated with brief dives during the same recording session (Figures 2, 4). In seven of the eight trackings in which both speed and depth were telemetered, and where tracking extended at least into dusk, the highest mean speeds occurred at relatively great depths (means: 4.8 km/h, 69 m) while the lowest speeds occurred at much shallower depths (means: 0.5 km/h, 20 m). This suggests that some factor in deeper water stimulated this speed increase, possibly presence of food.

Swimming Direction

Figure 5 shows clearly the relationship between swimming speed and rate of movement throughout the diel cycle. As expected, swimming speeds had the higher values, as the two measures would have been equal only in cases where the shark swam in a straight line for the entire 30-min interval between position determinations. During daylight hours both rates were moderately close, suggesting that the sharks made gradual changes in swimming direction rather than abrupt

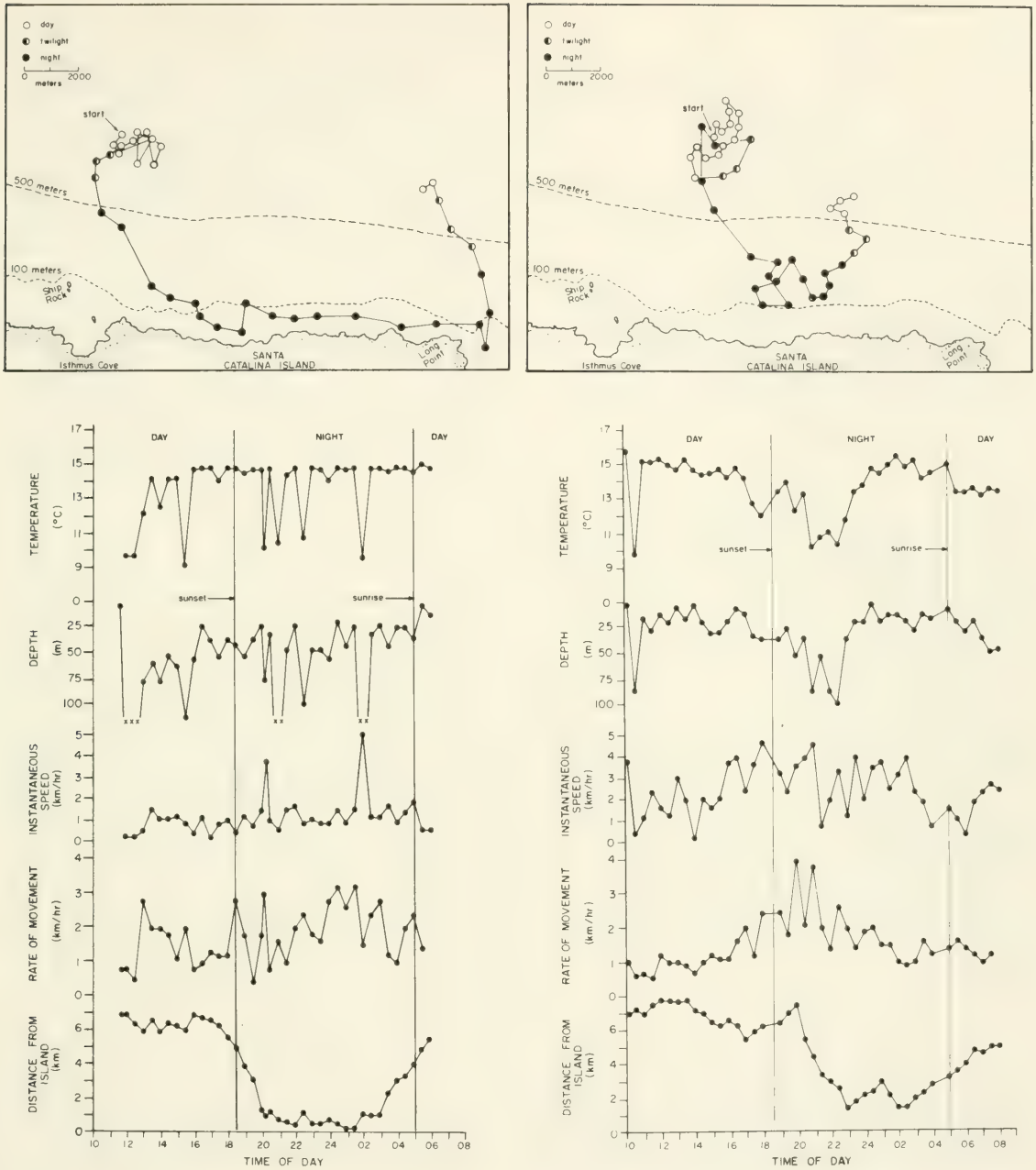

FIGURE 2.—Data from two individual trackings of blue sharks typical of the late March to early June period. Top, shark positions at approximately 0.5-h intervals. Bottom, telemetered sensor data. Note the characteristic evening-twilight migration towards the island, the initial plunge occurring immediately after transmitter application, and the close correlation between temperature and depth. Depths in excess of 110 m (the sensor limit) are indicated by ××.

changes. During the dusk transition, rate of movement most closely matched swimming speed, indicating the greatest consistency in swimming direction. In timing, this coincides with the relatively oriented shoreward migrations of from late March to early June. The greatest disparity be-

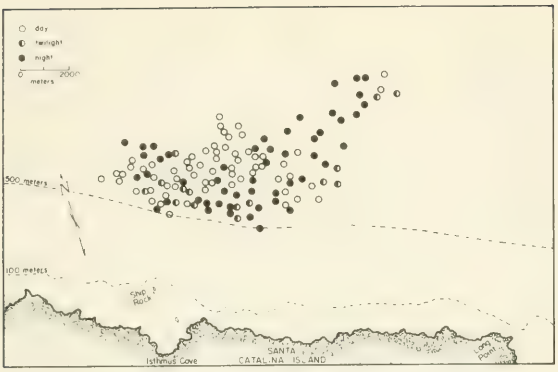

FIGURE 3.—Positions of three blue sharks tracked from late June to early October 1972. Note that both day and night positions are well offshore over relatively great depths.

tween rate of movement and swimming speed was during the early evening, evidence that much of the swimming then was variable in direction—a possible indication of searching for and/or pursuing prey. Beginning in the early morning and continuing through dawn, the differences between the two rates lessened.

A compass sensor for direct measurement of instantaneous swimming direction (azimuth) was incorporated during only one successful tracking. The compass data from this tracking (Figure 4) show that the greatest number of multiple-direction recordings (i.e., during single-recording periods) occurred at night, suggesting that variability of swimming direction is generally greater at night. During one nighttime recording, a change of at least 360° coupled with a speed change of 1 to 5 km/h was noted during one 15-s period.

Vertical Movement

Figure 6 illustrates the mean depths telemetered from all sharks with transmitters equipped with depth sensors. The sharks were within a depth range of 18 to 42 m for 92% of the time; they appeared to equal or exceed 100 m only during 3.9% of the readings (excluding initial plunges). The apparent tendency was a slight increase in mean depth at night. The mean daytime depth was 30 m; at night 40 m. Individual tracking graphs show that the sharks covered the entire depth range of the sensors (0–110 m) during both day and night, but that at night there were more vertical excursions from shallow to deep, i.e., greater variability in depth. During four trackings, the sharks may have been close to the bottom when in the relatively shallow water near the island.

The first hour of depth data were excluded from Figure 6 because of what appears to be an initial plunge induced by tagging trauma. As shown in Figure 7, the data also suggest that this initial effect decreased or disappeared within 1.5 h after tagging. About half of the sharks tagged exhibited this "abnormal" plunge (to a mean depth of at least 95 m) within 0.5 h of being tagged. The others apparently did not—possibly a result of the tag dart penetrating in a less sensitive spot. Of the first nine sharks tagged, six were seen to return to the bait cannister within seconds after transmitter application—suggesting little, if any, tagging trauma. Two of these six sharks, however, still made a deep dive by the next recording session.

Temperature

Blue sharks in the study area appeared to prefer a relatively narrow range of water temperatures. Overall, the telemetered sharks were found in a temperature range of 8.5° to 17.5°C, but occurred in the much narrower range of 14.0° to 16.0°C for 73% of the time. Seasonality of diel depth/temperature selectivity was not apparent from either the temperature or depth data. As expected, the telemetered depth and temperature data usually corresponded quite well, i.e., an increase in depth accompanied by a decrease in temperature (Figures 2, 4). Individuals were most often seen swimming at the surface during the cooler months, but rarely during either the coldest or warmest months, a behavior that may have been influenced by surface temperatures.

DISCUSSION

It is not surprising that the blue shark appears more active at night than during the day. Carcharhinids in general are considered by Randall (1967) to be nocturnal. In addition, most sharks studied quantitatively in this regard have proven to be basically nocturnal, the bonnethead shark studied by Myrberg and Gruber (1974) being a possible exception. Like other nocturnal sharks, however, blue sharks certainly feed diurnally at times, and it is common knowledge that they readily respond to opportunistic feeding stimuli (e.g., bait) during the day. There have also been observations of blue sharks feeding naturally during

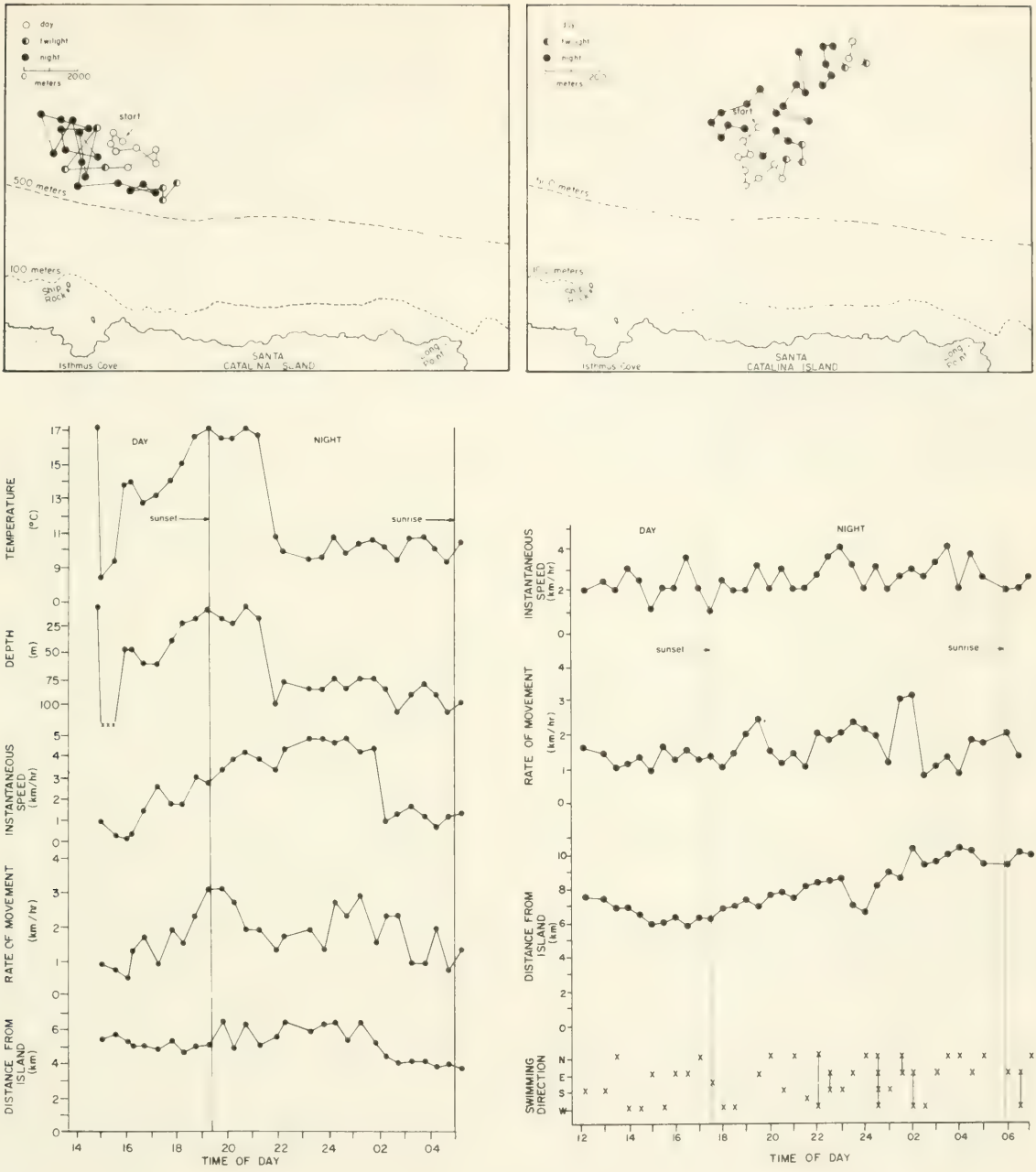

FIGURE 4.—Data from two individual trackings of blue sharks typical of the late June to early October period. Top, shark positions at approximately 0.5-h intervals. Bottom, telemetered sensor data. Note the absence of shoreward movement, the increased swimming speed and depth at night (left), and the greater frequency of sudden direction change, i.e., multiple-direction recordings, at night (right).

the day, e.g., on blacksmith, *Chromis punctipinnis* (R. R. Given pers. commun.; D. R. Nelson unpubl. data) and on northern anchovy, *Engraulis mordax* (T. C. Sciarrotta unpubl. data).

The large size of the blue shark's eye suggests adaptation to low light, as in general, nocturnal fishes have relatively large eyes. However, large eyes are also associated with moderately deep

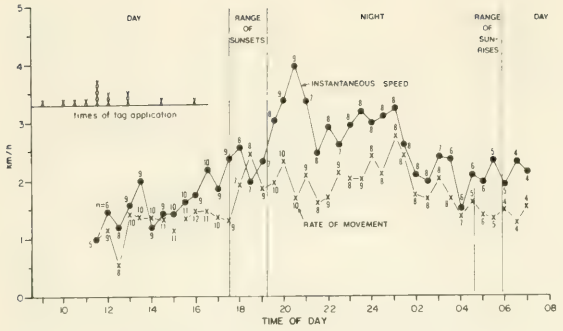

FIGURE 5.—Comparison of mean rate of movement (all sharks) and telemetered swimming speed (sharks with speed sensors) for blue sharks. Note the increase in both parameters at night, the greater values for swimming speeds (as expected), the close similarity during times corresponding to shoreward movements (relatively straight swimming), and the large disparity in early evening (relatively nonstraight swimming).

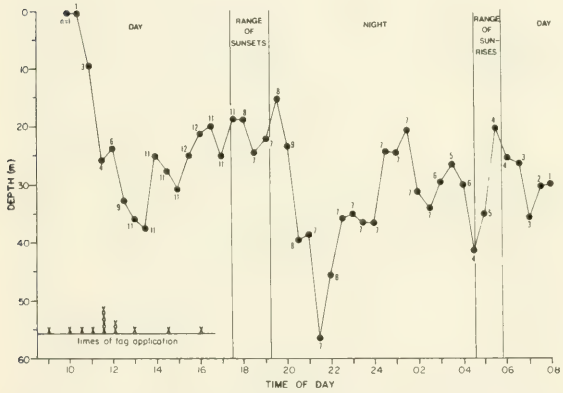

FIGURE 6.—Mean depths of all blue sharks tracked with transmitters having depth sensors. The first hour of each tracking is deleted because of the initial plunge in response to tag application. Note the generally greater depths at night.

habitat (mesopelagic), but since the blue shark's habitat appears relatively shallow (epipelagic), the large eye would seem best suited to visual hunting at night.

It is known that cephalopods and small pelagic fishes form a major part of the diet of blue sharks (Strasburg 1958; Stevens 1973; Tricas 1977). The observed seasonal differences in diel movement patterns (Figures 1, 3) may reflect differences in type or location of prey. Fishery landings of market squid, *Loligo opalescens,* were high during February to June 1972, but low from July to December (Pinkas 1974), thereby indicating the inshore presence of spawning congregations (Frey

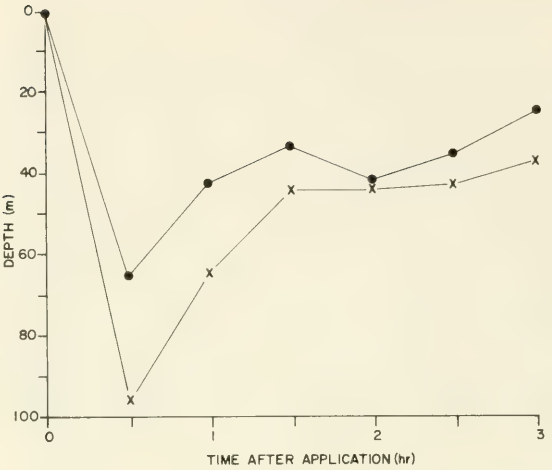

FIGURE 7.—Mean depths of blue sharks for the first 3 h of each tracking. Upper curve, all 12 sharks carrying transmitters with depth sensors. Lower curve, seven sharks judged to have made an "abnormal" plunge in response to the trauma of tag application. Note that the initial depth response appears to have subsided by the recording session 1.5 h after application.

1971), which are susceptible to commercial fishermen using night-lighting techniques. Cousteau and Cousteau (1970) described blue sharks gorging themselves on spawning squid that were light-attracted to the surface near their vessel.

The evening-twilight onshore movements which occurred during March to early June may be due to the nearshore abundance of squid and a possibly reduced availability of prey offshore. Conversely, the offshore pattern from late June to October may be a result of reduced squid population nearshore, but increased populations of jack mackerel, *Trachurus symmetricus,* and anchovy offshore. The limited stomach-content data collected during this study support this hypothesis.

In regard to depth/temperature preferences, the results of Strasburg (1958) are somewhat different from those of the present study. His longline catches of blue sharks at equivalent latitudes were from depths of 53 to 93 m (45%), 93 to 143 m (30%), and 123 to 166 m (25%). The blue sharks tracked in the present study appeared to exceed 93 m only about 5.1% of the time (excluding initial plunges). It is conceivable, however, that Strasburg's percentages may have been influenced by the sharks being attracted deeper than normal by the sloping odor corridors from baits on the gradually sinking longlines. That blue sharks on occasion go even deeper than Strasburg's deepest hooks was noted by Pethon (1970) who reported captures in Norwe-

gian waters from depths as great as 370 m. Davies and Bradley (1972) observed individuals at depths between 100 and 275 m during a descent in the submersible *Deepstar 4000*. A large school of northern anchovy was also observed in this depth range and a predator-prey relationship was suggested, although the possibility of the sharks following the descending submersible could not be eliminated.

In regard to temperature, Strasburg (1958) recorded 99% of his catches over the range of 7° to 20°C, with 67% between 10° and 15°C. Thus, temperature alone may not be reason for the apparent absence of blue sharks from the offshore study area during January and February 1972 when the surface temperature was about 13°C.

The navigational mechanism employed by the sharks during their island-oriented migration is unknown. Traditional explanations for such fish movements include sun-compass orientation, visual landmark recognition, and orientations to chemical or thermal gradients. None of these mechanisms seem plausible in view of the constancy of the pelagic environment, depths usually occupied during the movement, and the relative darkness in which the movements often occurred. Orientation to magnetic or electric fields is one possibility that must be considered in view of the recent findings of Kalmijn (1971, 1973) demonstrating magnetic/electric responses in sharks of adequate sensitivity for such a mechanism. Another possibility is orientation by passive acoustic means to the sounds of the island shoreline, in a manner similar to that suggested by Evans (1971) for dolphins.

The diel inshore-offshore migration shown by this study must also be considered in view of the much longer range movements exhibited by blue sharks. Individuals off California are known to segregate by sex, and seasonal changes in sex ratios imply seasonal north-south migration, perhaps in response to water temperature (Johnson 1974; Bane 1968; Tricas 1977). Tagged individuals have exhibited some very long-range movements. One blue shark tagged by Bane off Newport Beach, Calif. in July 1967 was recovered in December of the same year about 1,300 km west of Nicaragua. Another tagged by D. R. Nelson (unpubl. data) off San Diego, Calif. in October 1966 was recovered in October 1969 about 1,800 km west of the Galapagos Islands, a distance of 4,000 km from its tagging site. This shark was captured only 8 days short of a full 3 yr at liberty and, therefore, did not appear to be participating in any seasonal north-south migration. Both of the above sharks were recovered by Japanese fishing vessels, presumably longlining in relatively deep, cool water.

ACKNOWLEDGMENTS

We sincerely thank the many persons who contributed to this study, especially E. Standora (initial development and testing of telemetry system), H. Carter and D. Ferrel (circuit design), and J. Hall (assistance during trackings at sea). We also acknowledge the Office of Naval Research for financial support, through contract N00014-68-C-0318, under project NR-104-062, for the program of shark research of which this study is a part.

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A BIOENERGETIC MODEL FOR THE ANALYSIS OF FEEDING AND SURVIVAL POTENTIAL OF WINTER FLOUNDER, *PSEUDOPLEURONECTES AMERICANUS*, LARVAE DURING THE PERIOD FROM HATCHING TO METAMORPHOSIS

GEOFFREY C. LAURENCE[1]

ABSTRACT

A bioenergetic model was developed which simulated effects of temperature, prey density, and larval size on ability of winter flounder, *Pseudopleuronectes americanus*, larvae to obtain food energy to provide for experimentally determined growth and metabolism. Larval feeding at constant temperature and as a function of prey concentration was exponential and more sharply asymptotic in younger fish than in those near metamorphosis. Specific growth rates were exponentially related to prey concentrations and ranged from 5.72 to 8.70%/day at survival prey concentrations of 3.7 to 21.7 cal/liter. Daily required feeding time was directly related to prey availability. Critical plankton densities below which larvae did not have enough time during the day to obtain adequate food for growth and metabolism varied with age and ranged from 2.1 to 5.7 cal/liter. Simulated physiological energy utilization and required caloric food intake were inversely related to prey concentration and varied with larval stage of development. Food requirements expressed as numbers of copepod nauplii consumed per day ranged from 19 for first feeding larvae to 235 for metamorphosed juveniles. Predicted gross growth efficiencies were directly related to prey concentration and increased with age from 5 to 33%. All indications pointed to a "critical period" of larval survival during the period of exogenous feeding initiation and immediately after.

One of the important problems in fishery research and management is identifying and understanding the functional mechanisms of the stock–recruitment relationship. It is becoming more apparent that focusing attention on studies of mortality in the early life stages, particularly the larval stage, may help in this understanding. Mortality rates are usually the highest and most variable from year to year during the early life stages. Because of this, even small changes in mortality during this period can produce a magnified effect on the eventual numbers of recruits to sport or commercial fisheries.

Other than predation, the most important probable factors influencing larval mortality are food and feeding relationships and the influence of environmental parameters on these processes. The acquisition of the required food ration by fish larvae is of prime importance in survival and successful development. Without the proper quantity and quality of food, larvae will be adversely affected and survival will be influenced. Bioenergetic relationships have been studied extensively for adult fishes, and the works of Ivlev (1939a, b, c), Winburg (1956), Paloheimo and Dickie (1966a, b), and Warren and Davis (1967) are among the most complete. However, the use of energy resources in physiological mechanisms and the relationships of feeding, growth, and survival in the early life stages of fishes have only recently been studied (Ivlev 1961a, b; Lasker 1962; Laurence 1969, 1973).

It is the object of this research to examine the effects of food and feeding on winter flounder, *Pseudopleuronectes americanus*, survival from the period of hatching to metamorphosis and to develop a model of these critical processes. The model includes the forcing variables of temperature, prey density, and larval size or age and their effects on the ability of winter flounder larvae to successfully acquire energy rations necessary for experimentally determined growth and metabolic parameters. The energy rations are quantified as to caloric value of ration, numbers of specific prey organisms consumed, time for required intake, and metabolic parameters dealing with conversion into fish flesh.

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MATERIALS AND METHODS

Adult winter flounder were captured by trawl net from Narragansett Bay, R.I., and maintained in 1,900-liter experimental aquaria. Embryos were obtained by allowing the fish to ripen naturally under optimum temperature and photoperiod conditions or causing ovulation with hormones according to the techniques of Smigielski (1975). Embryos were incubated with methods developed at the Narragansett Laboratory (Smigielski and Arnold 1972).

All experiments and rearing were done at 8°C during these studies since this temperature is the approximate mean temperature for the entire period from hatching to metamorphosis for winter flounder in the Narragansett Bay area. Stock cultures of larvae were reared in series of black 64-liter experimental aquaria. The aquaria were placed in an environmental room or in water baths where the temperatures were maintained by program recorders controlling heating and cooling coils. All experimental aquaria were aerated with air stones and were semiclosed systems with a portion of the seawater being replenished every 1 or 2 days. Illumination was controlled by timers which provided a 12:12 day–night photoperiod corresponding to the mean photoperiod during the normal winter flounder spawning time.

Zooplankton fed during all experiments consisted mainly of the nauplii, copepodites, and adults of the copepods *Acartia clausi, Centropages hamatus,* and a few *Temora longicornis* and *Eurytemora affinis* collected from the Narragansett Bay area with 0.5-m plankton nets fitted with 64- and 116-μm mesh. Collections were sieved through 200- or 500-μm mesh strainers, depending on the size of larvae to be fed. Plankton densities in experimental aquaria were monitored by taking two to four 5-ml aliquots from the aquaria and counting the number of plankters under a dissecting microscope.

The relationship between larval size (body dry weight) and stomach contents was studied from hatching to metamorphosis. Larvae were reared in a 64-liter black aquarium and were fed high prey concentrations of 13.6–20.5 cal/liter or approximately 2 or 3 nauplii/ml. Samples of 25 larvae were taken each week until metamorphosis for stomach analyses and dry body weight determinations.

Experiments determining the influence of prey concentration on daily feeding intensity expressed as stomach contents were conducted at 0.68, 3.41, 6.80, 20.5, 34.1, and 47.8 cal/liter (corresponding to 0.1, 0.5, 1.0, 3.0, 5.0, and 7.0 nauplii/ml). Larvae aged 2, 5, and 7 wk after hatching were used. Approximately 25 larvae were placed in all black 4-liter aquaria containing the desired prey densities. The larvae were allowed to feed for 1 day's photoperiod (12 h) after which they were pipetted onto a 100-μm mesh screen and allowed to suffocate to prevent regurgitation of food before being preserved in 5% Formalin.[2] Ten larvae from each prey concentration were used for stomach analyses and 10 were used for mean dry body weight determinations. Stomach analyses were done with a dissecting microscope. Larval stomachs and intestines were teased apart with fine needles, and contents were identified to genus and species if possible.

Digestion rate measured by gut clearance time of larval winter flounder at 8°C was determined by feeding dyed zooplankton according to the techniques of Laurence (1971a). Transparency of the larvae permitted visual observation of dyed plankters in stomachs of living larvae. To determine the evacuation time of the stomach and intestine under active feeding conditions, larvae feeding on dyed plankters at concentrations of 1 or 2 nauplii/ml were removed and placed in duplicate aquaria with similar concentrations of nondyed plankton, and the gut clearance times of the dyed plankters from individual larvae were recorded.

Experiments determining the influence of temperature on growth of winter flounder larvae were conducted in 38-liter experimental aquaria. Feeding, monitoring, and sampling techniques and results for these experiments are described in detail by Laurence (1975).

The influence of planktonic prey concentration on growth and survival at 8°C from the period hatching to metamorphosis was studied at prey concentrations of 0.068, 0.68, 3.41, 6.80, and 20.5 cal/liter, corresponding approximately to 0.01, 0.1, 0.5, 1.0, and 3.0 nauplii/ml. Larvae were stocked at an initial density of 500 per aquarium; methods for maintaining prey concentrations, sampling, and determining growth and survival rates are described in detail by Laurence (1974).

Standard manometer equipment (Warburg res-

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

pirometers) and techniques (Umbreit et al. 1964) were used to measure oxygen consumption for metabolic determinations in relation to temperature and larval size. A description of the specific methods and results has been reported earlier (Laurence 1975).

All combustions for caloric determinations of larval winter flounder tissue were done in triplicate in a Parr 1241 automatic adiobatic calorimeter adapted for a microbomb. Caloric values for copepod prey species and methodology for these determinations are reported by Laurence (1976).

All statistical analyses used in this research are described in Steel and Torrie (1960) and Draper and Smith (1966). Modeling and analyses were done in the FORTRAN IV language on an IBM 370 computer.

EXPERIMENTAL RESULTS

Food Consumed and Relationship to Larval Size

Numerical analysis of stomach contents is not very meaningful in itself. It can, however, be useful in conjunction with the measurement of other parameters. An estimation of the dry weight and caloric value of food consumed per larval dry weight was needed as part of the overall bioenergetic model. Stomach analysis by enumerating copepods in larvae fed high concentrations (2 or 3 nauplii/ml) combined with information on dry weights and caloric values of the copepods provided this. Mean dry weights for the copepod species and life stage were taken from the literature (Conover 1960; Anraku 1964; Hargrave and Geen 1970; Gaudy 1974). Caloric values were determined in our laboratory (Laurence 1976). The average composite values used for the copepods in this study were 1.3 μg dry weight for nauplii, 15.4 μg dry weight for older stages, and 5,251 cal/g dry weight for all copepod tissue. Multiplying the numbers of plankton species and life stage per stomach by the average dry weight values for each plankter type and summing yielded the mean dry weight of the stomach contents. Results of these analyses along with nauplii to older stage ratios of copepods consumed and caloric value per stomach are shown in Table 1. The regression relationship of the logarithms of larval dry body weight and larval stomach contents weight was positively linear (Figure 1) and significantly correlated ($R = 0.87$, $P = 0.01$).

TABLE 1.—Mean numbers, weights, and caloric values of copepods consumed by larval winter flounder of different sizes. Each sample consists of 25 larvae.

Mean larval dry wt (μg)	Mean no. of copepods per stomach	Nauplius to older stage ratio	Mean dry wt per stomach (μg)	Calorie per stomach
10.4	2.0	1:0	2.6	0.0137
14.3	1.0	1:0	1.3	0.0068
21.5	2.1	1:0	2.7	0.0142
29.4	5.4	1:0	7.0	0.0368
51.1	3.3	29:1	6.0	0.0315
81.2	32.3	12:1	41.9	0.2205
226.8	2.9	12:1	6.9	0.0362
396.6	4.7	3:4	43.8	0.2300
444.2	33.5	22:1	57.7	0.3030
513.9	8.4	1:2	89.9	0.4720
667.6	3.0	1:2	32.1	0.1686

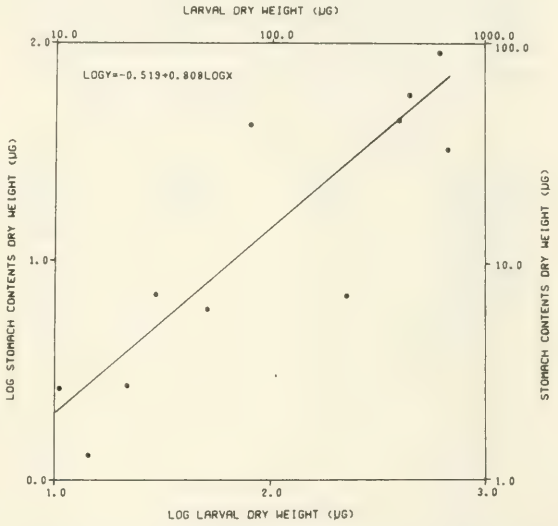

FIGURE 1.—The regression relationship of larval dry body weight to larval stomach contents weight for winter flounder at 8°C.

Prey Density and Intensity of Feeding

The relationship between intensity of feeding and concentration of prey is important in determining food intake. Ivlev (1961b) has analyzed this relationship and expressed it by the following function:

$$\frac{dr}{dp} = \alpha(R - r)$$

where r = size of a unit ration for a unit time
R = maximum size of the ration during the same unit time at the upper limiting level of food concentration beyond which ration size does not increase

α = coefficient of proportionality
p = plankton concentration.

After integration, the function becomes:

$$r = R\ (1 - e^{-\alpha p}).$$

Use of this relationship in analyzing winter flounder feeding as influenced by prey densities of 0.68–47.8 cal/liter, or 0.1–7.0 nauplii/ml, yielded some interesting results (Figure 2). Feeding was reasonably constant in the youngest fish with an asymptote being reached quickly at the lower prey concentrations. Five-week-old larvae displayed a rather classic form of the Ivlev curve with food intake increasing with prey density, reaching a maximum at approximately 6.8 cal/liter or 1.0 nauplius/ml, and then remaining quite stable. The oldest larvae, prior to metamorphosis, showed an increasing food intake through the whole range of plankton densities, right up to 47.8 cal/liter or 7.0 nauplii/ml. In general, there appeared to be an increasing of the upper limiting level of food concentration and a decreasing of the coefficient of proportionality (α) with increasing larval age.

Digestion Rate

Winter flounder larvae were known to be continuous, visual daylight feeders from prior research. Preliminary attempts at establishing digestion rates and unpublished results of night feeding experiments showed that larvae at-

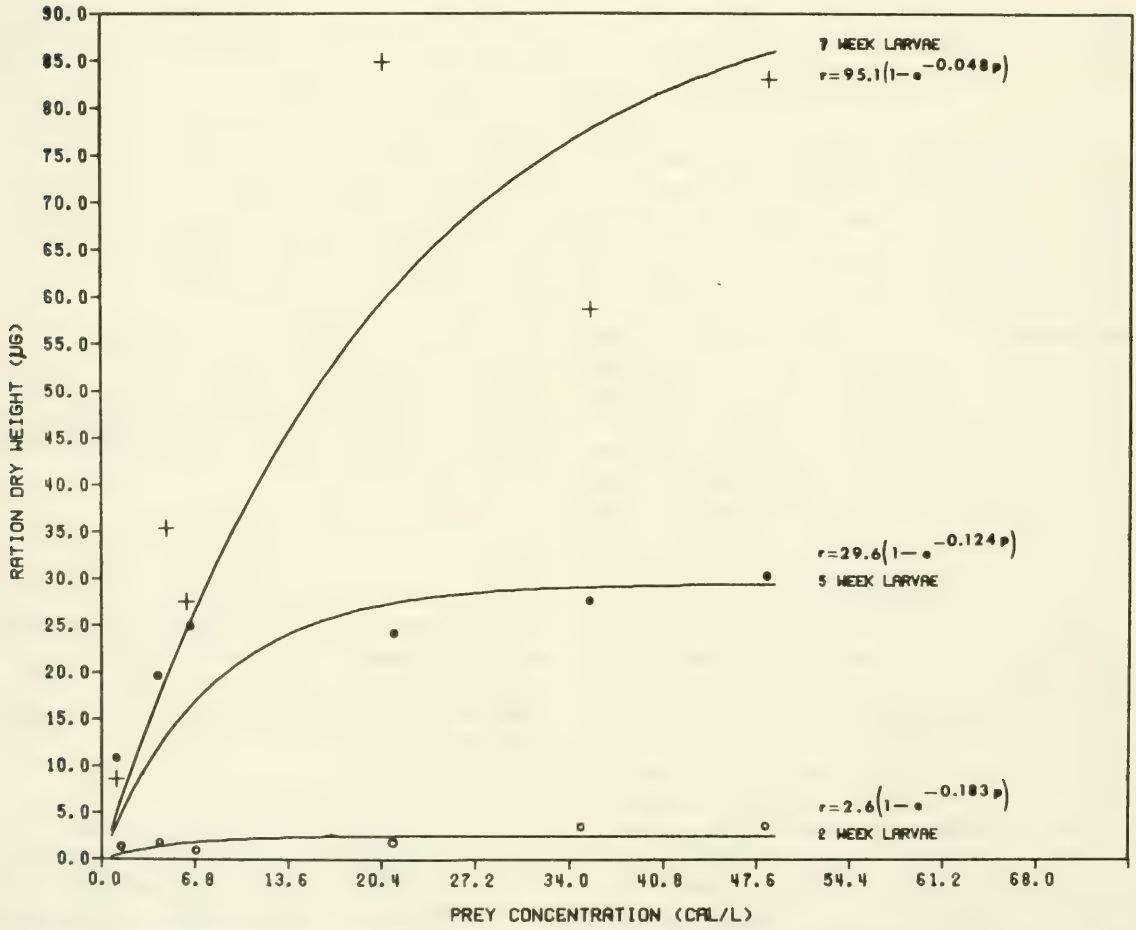

FIGURE 2.—The relationship between planktonic prey concentration and feeding intensity expressed as stomach ration for different aged winter flounder larvae at 8°C.

tempted to feed constantly under daylight conditions and ceased feeding entirely during darkness. Evacuation rates of the gut while larvae were actively feeding were recorded at 8°C for estimates of digestion rates. Results of 10 individual larvae showed a mean, active digestion time of 6.6 h with a range of 5.1–8.4 h.

Effects of Prey Density on Growth and Survival

The effects of five prey densities from 0.068 to 20.5 cal/liter (approximately 0.01–3.0 nauplii/ml) on growth and survival of winter flounder larvae from hatching to metamorphosis at 8°C were examined. Larval survival did not exceed 2 wk at the lower two densities of 0.01 and 0.1 nauplius/ml. Growth expressed as dry weight against time at the three survival densities (3.4, 6.8, and 20.5 cal/liter) was similar (Figure 3), as indicated by the confidence intervals about the slopes of the descriptive regression equations (Table 2). Specific growth rates on a daily basis increased with plankton concentration and were experimentally observed to be 8.62%/day for 3.0 nauplii/ml, 7.68%/day for 1.0 nauplius/ml, and 5.72%/day for 0.5 nauplius/ml.

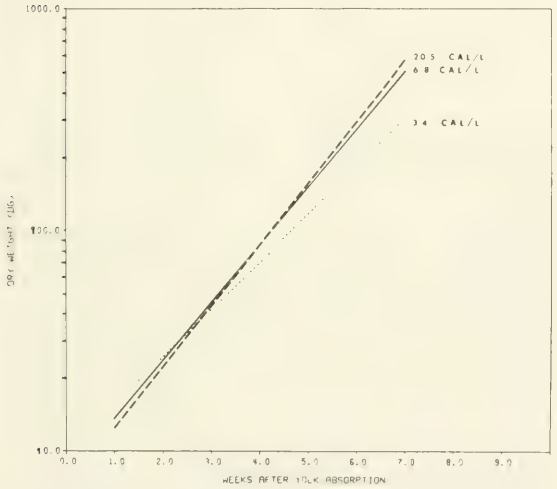

FIGURE 3.—Growth of winter flounder larvae at 8°C and at three different planktonic prey densities.

TABLE 2.—Regression equations and statistical parameters of winter flounder dry weight growth vs. time at 8°C and different planktonic prey densities.

Planktonic concentration (cal/liter)	Growth regression equation	Confidence interval about slope	Correlation coefficient
20.5	$\log Y = 0.849 + 0.269X$	0.212–0.326	0.98
6.80	$\log Y = 0.830 + 0.272X$	0.234–0.311	0.99
3.41	$\log Y = 0.990 + 0.208X$	0.141–0.275	0.97
0.68	No survival to metamorphosis		
0.068	No survival to metamorphosis		

Plankton density influenced survival more significantly than growth. Specific mortality coefficients calculated by the methods of Laurence (1974), which correct for the number of experimental removals for growth measurements, demonstrated a direct relationship with lower mortality rates at each higher plankton density (Table 3). Plots of predicted specific mortality coefficients through the range of plankton densities from 0.68 to 20.5 cal/liter based on the above results yielded an exponential relationship (Figure 4).

TABLE 3.—Daily mortality coefficients of winter flounder at 8°C as influenced by planktonic prey density.

Planktonic concentration (cal/liter)	Corrected number of survivors out of 500	Days of survival[1]	Specific mortality coefficient
20.50	171	49	0.022
6.80	19	49	0.069
3.40	13	42	0.091
0.68	5	15	0.307

[1]No calculable survival at the lowest plankton density of 0.068 cal/liter.

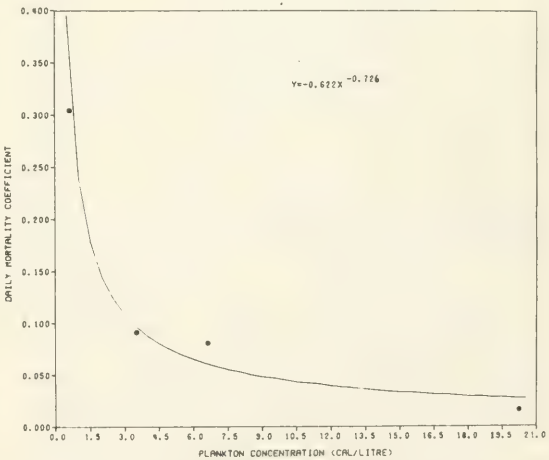

FIGURE 4.—Daily mortality coefficients of winter flounder at 8°C from the period hatching to metamorphosis as influenced by prey density.

Metabolic Rate

Laurence (1975) expressed metabolism of winter flounder from hatching through metamorphosis in terms of oxygen consumption. Regression relationships of mean hourly oxygen

consumption in microliters from hatching through and beyond metamorphosis on dry body weight were nonlinear and fitted best by a third-degree polynomial (Figure 5 from Laurence 1975). A third-degree polynomial was statistically most significant, as indicated by analysis of variance (F = 13.2 for cubic term, 7.4 for quadratic term, and 9.5 for linear term) over the weight range studied (10–4,000 μg). However, in this research the size range for larvae was 10–1,000 μg, and only the predicted data from the first ascending leg of the polynomial at 8°C were used in the computations.

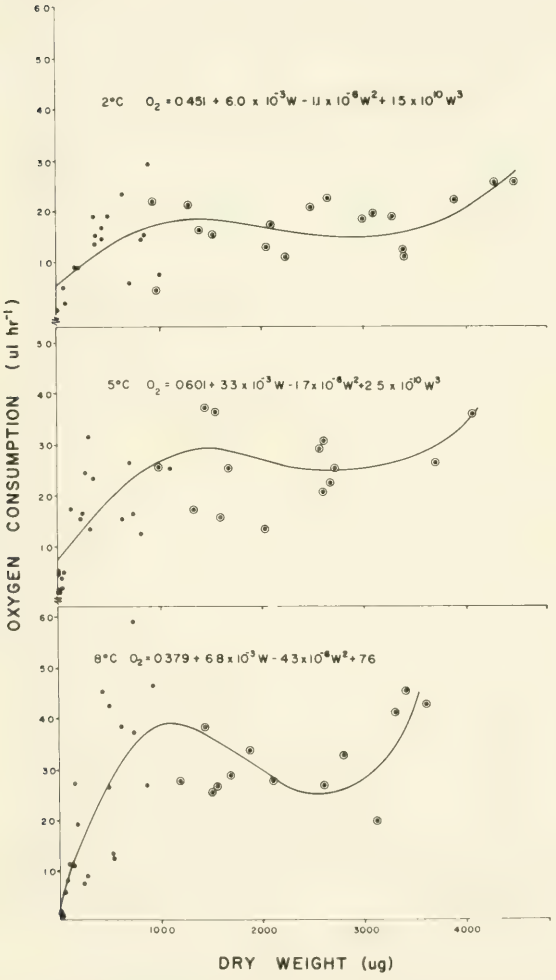

FIGURE 5.—Regression of mean hourly oxygen consumption on dry weight of winter flounder larvae and juveniles at three temperatures. Circled data points indicate metamorphosed juveniles. Results at 8°C used in these studies. (From Laurence 1975.)

BIOENERGETIC MODEL

A general model for the transformation of food to fish flesh and the energy relationships involved has been discussed in detail by Winburg (1956) and Warren and Davis (1967). The basic relationship can be expressed as:

$$Q_+ = Q_- + Q' + Q_- \quad (1)$$

where Q_+ = energy of food consumed
Q_- = energy of waste products in feces and urine
Q' = energy of growth
Q_- = energy of metabolism.

Since a portion of the energy value of food is lost in the feces and urine and not utilized or assimilated, Winburg (1956) proposed the following "balanced equation":

$$Q_+ - Q_- = Q' + Q_- \quad (2)$$

or

$$bQ_+ = Q' + Q_- \quad (3)$$

where b = the coefficient of utilization or, in Brody's (1945) terminology, the physiological useful ration. Equation (3) analyzes the conversion of food energy inside the fish (physiological). However, influences of the environment on food consumption and utilization must also be considered. Many modifications based on my experimental results and additions of methods of other researchers have been incorporated into a model suitable for a broader analysis of the bioenergetics of winter flounder larvae. The following paragraphs present a detailed description of the methods used to derive this model.

Ivlev (1961b) formulated a model founded on the basic bioenergetic equation (Equation (3)) for the utilization of food by plankton-eating fishes. The relationship is:

$$0.7Q_+ = Q' + Q_-. \quad (4)$$

The coefficient of utilization (b) is assumed to be 0.7, based on information provided by Ware (1975) who reviewed the most recent thinking of the efficiency of food conversion. During the course of a day, a larval fish will be active in daylight (while feeding) and relatively passive the remainder of the time (usually at night). It can be assumed that the intensity of metabolism dur-

ing rest is represented by the standard metabolic rate (Q_s) and active metabolism by the active rate (Q). Thus, if it is assumed that a fish actively feeds for a given number (a) of hours, the total daily expenditure of energy for metabolism can be defined as:

$$Q_- = a(Q - Q_s) + 24Q_s. \quad (5)$$

The basic Equation (4) can then be rewritten as:

$$0.7Q_+ = Q' + a(Q - Q_s) + 24Q_s. \quad (6)$$

Also, the energy of food consumed (Q_+) can be equal to the sum of the hourly rations, r (see Prey Density and Intensity of Feeding), or $Q_+ = ar$, and thus:

$$Q_+ = aR(1 - e^{-\alpha P}). \quad (7)$$

Solving Equations (6) and (7) simultaneously by equating the Q:

$$\frac{Q' + a(Q - Q_s) + 24Q_s}{0.7} = aR(1 - e^{-\alpha P}) \quad (8)$$

is obtained. Thus:

$$a = \frac{Q' + 24Q_s}{0.7R(1 - e^{-\alpha P}) - (Q - Q_s)}. \quad (9)$$

Deriving the value of a, a number of different parameters can be computed. They are: 1) critical plankton density below which growth, metabolism and subsequent survival would be adversely affected, 2) food intake, 3) energy expenditure, 4) nonassimilated energy, 5) growth efficiency, 6) percent body weight eaten, and 7) the number of a given plankton species and life stages eaten per day. The following is a step by step explanation of the modifications used to compute these parameters at 8°C for larval dry weight from 10 to 1,000 μg (corresponding to the time period hatching to metamorphosis), for plankton concentrations from 0.5 to 21.7 cal/liter (approximately 0.1–3.0 nauplii/ml), and for growth, metabolic and digestion rates observed in laboratory experiments at 8°C.

1. Stomach contents weight in micrograms of planktonic prey eaten by a given size larva was computed from the regression equation presented in Figure 1.

2. The stomach contents weight per hour, or weight of food consumed per hour, was calculated from a modification of Bajkov's (1936) digestion equation. The modified equation is:

$$F = \frac{ST}{H} \quad (10)$$

where F = weight of food consumed per hour
S = average weight of food in the stomach at the time of sacrifice
T = feeding time in hours
H = number of hours necessary for food to be evacuated from the stomach at a given temperature = 6.6 h at 8°C for actively feeding winter flounder larvae.

Unpublished experiments indicated that winter flounder larvae fed only in daylight hours. Therefore, it was assumed that T was equal to 12.0 h in these experiments, or the approximate number of mean daylight hours in the period mid-February to mid-April, when winter flounder spawn. Also, F was considered to represent the maximum ration of a larva, or R (Prey Density and Intensity of Feeding section, Equations (7)–(9)).

3. R was converted to a caloric value by multiplying by 0.0052519 cal, or the average caloric value/microgram of the copepod species inhabiting Narragansett Bay and serving as potential prey for winter flounder (Laurence 1976).

4. The coefficient of proportionality (α) in Equation (9) was found to change linearly in a negative manner with increasing larval size (see Prey Density and Intensity of Feeding) and was correspondingly adjusted.

5. The growth increment, Q', was computed by multiplying the weight of a larva by the specific growth rate at 8°C for the specified plankton density (see Effects of Prey Density on Growth and Survival). This was converted to calories by multiplying by 0.0050026, or the caloric value for winter flounder tissue as determined in laboratory combustion experiments with a bomb calorimeter.

6. Metabolism for a larva of given weight was calculated from the regression equations for oxygen consumption and weight (Laurence 1975; Figure 5) and converted to calories by multiplying by 0.005 which represents the caloric equivalent of 1 μl of oxygen for the full range of respiratory quotients associated with the utilization of fats,

carbohydrates, and proteins (Swift and French 1954). Active metabolism (Q) was derived by multiplying standard metabolism (Q_s) measured in the oxygen consumption experiments by 2.5. Fry (1947) showed that the active metabolism in small fishes was about twice the standard rate. More recently, however, Ware (1975) demonstrated in a re-analysis of Ivlev's (1961b) data that active metabolism calculated for a variety of growth rates and feeding densities could vary between 2 and 3 times the standard rate. Recognizing that active metabolism is a dynamic factor, it is not unrealistic to assume a multiplier of 2.5 times standard metabolism for an estimate of active metabolism.

7. The number of hours (a) a larva of given weight needed to feed to attain a given growth rate at a given temperature and plankton concentration was computed from Equation (9).

8. Since winter flounder larvae were observed in experiments to be visual feeders, the plankton densities for each weight which predicted 12.0 h feeding time (a) were identified. These were considered critical densities because feeding times longer than this were ecologically impossible due to unsuitable photoperiod.

9. Food intake in calories was computed from Equation (7).

10. Metabolism or energy expenditure was computed from Equation (5).

11. Nonassimilated energy was computed by subtracting the energies of growth (Q') and metabolism (Q_-) from the energy of food intake (Q_+).

12. Gross growth efficiency was calculated from the formula:

$$K_1 = \frac{Q'}{Q_+}$$

where K_1 = gross growth efficiency and Q' and Q_+ are as previously defined.

13. The percent body weight eaten per day was calculated by dividing the caloric value of food intake (Q_+) by the caloric value of the given body weight.

14. The number of naupliar or adult copepods consumed per day at the given parameters was calculated by dividing the caloric value of the food intake (Q_+) by the previously defined average caloric value for nauplii or adults.

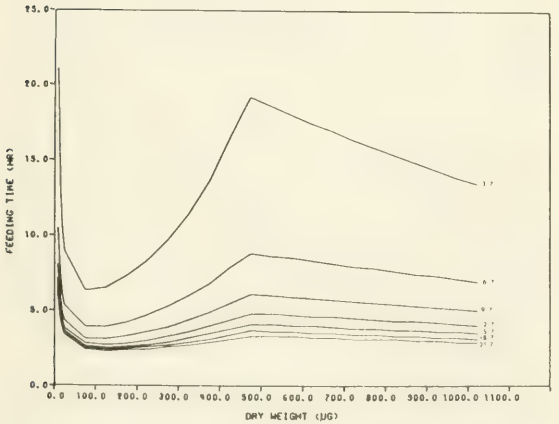

FIGURE 6.—Number of daily feeding hours required by winter flounder larvae to obtain energy for calculated growth and metabolism as influenced by larval dry weight and planktonic prey concentration at 8°C. Numbers for each simulated line indicate prey concentration in calories per liter.

MODEL SIMULATION RESULTS

Daily Feeding Time and Critical Prey Densities

The number of daily feeding hours required to meet growth and metabolism (a, Equation (9)) in relation to larval dry weight and at plankton densities which allowed feeding at some time within the limits of the 12-h day length simulated by the model is plotted in Figure 6. Feeding time at all plankton densities was initially high for the younger, smaller fish which later decreased before increasing again to a peak around 500 μg dry weight, or when metamorphosis starts to take place. A gradual decrease occurred during the metamorphosis period (500–1,000 μg larval dry weight). As was expected, required daily feeding times decreased with increasing prey density.

The critical, minimal prey densities below which longer than 12 h would have been required to obtain energy to meet growth and metabolism over the range of weights showed the highest critical densities during the period corresponding to first feeding with a decrease to a minimum shortly after (10–75 μg larval dry weight, Figure 7). An increase was then noted until the beginning of metamorphosis (500 μg) after which the critical prey density gradually decreased to complete metamorphosis (1,000 μg). The range of critical, minimum densities for the whole period was from 2.1 to 5.7 cal/liter, or approximately 0.3 to 0.8 nauplius/ml.

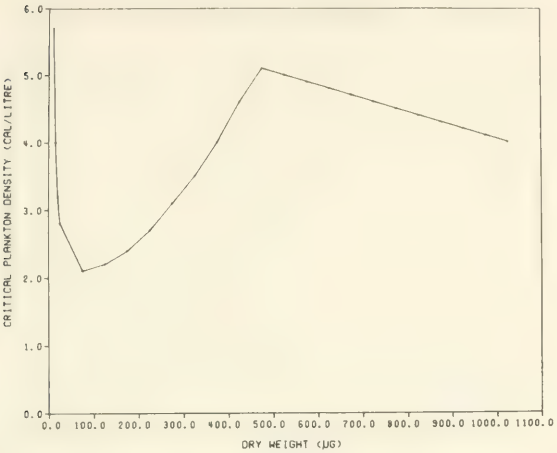

FIGURE 7.—Critical, minimum prey densities, below which feeding longer than the available photoperiod would permit to obtain energy for calculated growth and metabolic processes, over the weights range from hatching to metamorphosis for winter flounder at 8°C.

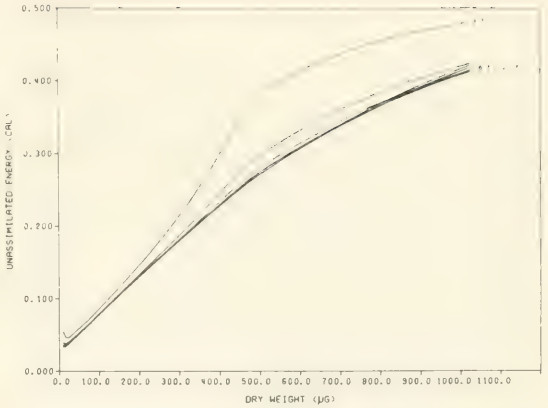

FIGURE 9.—Nonassimilated energy of winter flounder larvae at 8°C over the range of dry body weight from hatching to metamorphosis and at different planktonic prey concentrations. Numbers for each simulation indicate prey concentration in calories per liter; 6.7–21.7 cal/liter simulations are in ascending order from top to bottom.

Physiological Energy Utilization

Predicted daily metabolic energy utilized by winter flounder larvae from hatching to metamorphosis ($Q_{_}$, Equation (5)) showed a decrease shortly following hatching which later increased until initiation of metamorphosis when there was a leveling off (Figure 8). Energy expended was substantially higher at the lower prey concentrations with the differences minimized with increasing concentration. Predicted daily unassimilated energy, or energy not utilized in physiological processes and lost to the larval system, followed a similar trend to metabolic energy (Figure 9). In general, the ratio of nonassimilated to metabolic energy overall factor combinations was approximately 1:2.

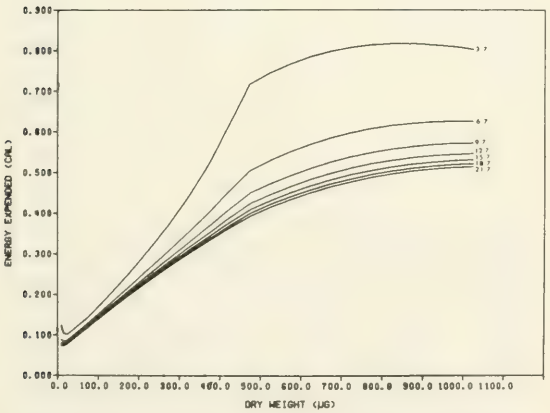

FIGURE 8.—Metabolic energy utilized by winter flounder larvae at 8°C over the range of dry body weight from hatching to metamorphosis and at different plankton concentrations. Numbers for each simulated line indicate prey concentration in calories per liter.

Required Food Ration and Growth Efficiency

Predicted daily caloric food requirements (Figure 10, Equation (7)) after an initial decrease following first feeding (10–30 µg dry weight) increased until the beginning of metamorphosis (500 µg), after which the rate of increase slowed until complete metamorphosis (1,000 µg). Food requirements were greater at lower prey concentrations with decreasing differences at higher concentrations. Conversion of caloric values of daily food requirements by division by mean caloric values of the copepod life stages per unit weight showed the numbers of nauplii or older stages necessary for consumption (Figure 11). Actual feeding experiments demonstrated that larvae do not prey entirely on one particular copepod life stage. The stages they consume are more a function of larval and copepod size. Smaller larvae initiate feeding on nauplii and gradually eat increasingly greater percentages of

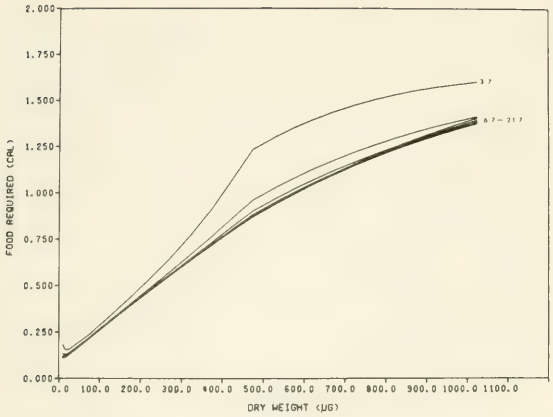

FIGURE 10.—Daily food requirements of winter flounder larvae at 8°C over the range of dry weight from hatching to metamorphosis and at different planktonic prey concentrations. Numbers for each simulation indicate prey concentration in calories per liter; 6.7–21.7 simulations are in ascending order from top to bottom.

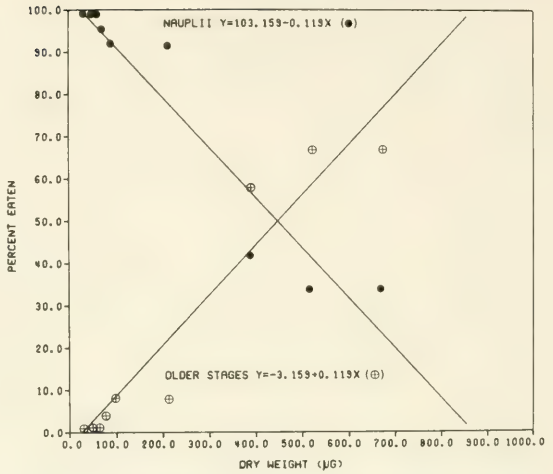

FIGURE 12.—Regression relationships of percentages of nauplii and older stage copepods eaten by winter flounder larvae of different sizes at 8°C.

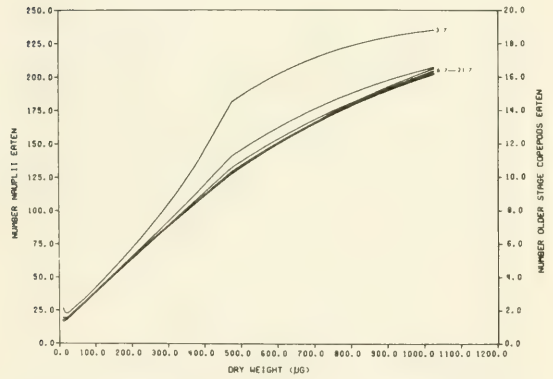

FIGURE 11.—Predicted number of nauplii or older stage copepods required for daily consumption by winter flounder larvae at 8°C over the range of dry body weights from hatching to metamorphosis and at different planktonic prey concentrations. Numbers for each simulation indicate prey concentration in calories per liter; 6.7–21.7 simulations are in ascending order from top to bottom.

older stage copepods as larval size increases (Figure 12).

The percentage of body weight consumed per day index (Figure 13) demonstrated sharply decreasing values during the first weeks of life (10–75 µg), after which values remained fairly stable until metamorphosis. More food was consumed per body weight at lower plankton densities. The differences became minimal with increasing plankton density.

Predicted gross growth efficiencies increased sharply from first feeding until a dry body weight of 100 µg, after which they continued to increase but at a decelerated rate (Figure 14). Efficiencies were lower at lower plankton concentrations, and the differences became smaller as plankton concentration increased.

DISCUSSION

A majority of the prior research has dealt with instantaneous estimates of larval food needs (Chiba 1961; Braum 1967) rather than a descriptive relationship over the range of larval sizes from hatching to metamorphosis. Larval winter flounder exhibited a linear increase in food consumption, as indicated by stomach contents with increasing size (Figure 1). A linear relationship was also reported for larval largemouth bass, *Micropterus salmoides* (Laurence 1971b). Stepien (1974) observed an exponential increase for the larvae of sea bream, *Archosargus rhombodalis*, at much higher temperatures (23°–29°C) than the 8°C studied for winter flounder in this research.

The amount of food a larval fish consumes during a day depends on the size of the fish and density of the prey organisms available (Ivlev 1961a, b). This is especially evident for winter flounder larvae for which the traditional Ivlev relationship changes with age or size (see Prey Density and Intensity of Feeding, Figure 2). Smaller, younger larvae reached maximum ration (R, Equation (7))

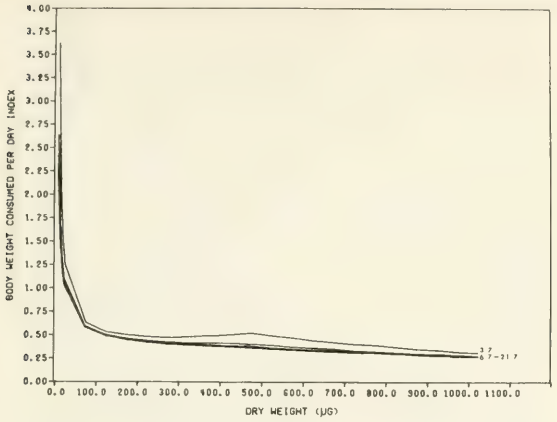

FIGURE 13.—Index of body weight consumed per day by winter flounder larvae at 8°C over the range of dry weights from hatching to metamorphosis and at different planktonic prey concentrations. Numbers for each simulation indicate prey concentration in calories per liter; 6.7–21.7 simulations are in ascending order from top to bottom.

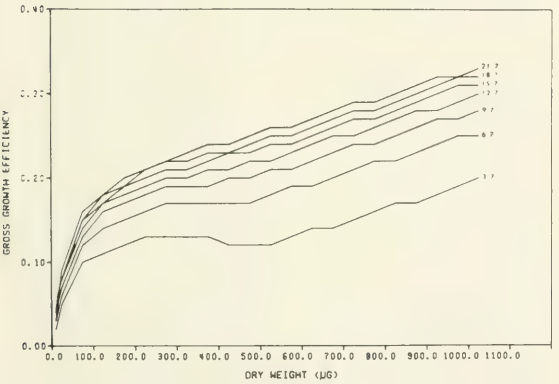

FIGURE 14.—Gross growth efficiencies of winter flounder larvae at 8°C over the dry body weights from hatching to metamorphosis and at different plankton concentrations. Numbers for each simulation indicate prey concentration in calories per liter.

at lower prey densities, while larger, older larvae approached maximum feeding ration at increasingly higher densities. The higher coefficient of proportionality (α, Equation (7)) values for the smaller larvae suggests that they have an easier time capturing their maximum ration. In fact, they reach their maximum ration at lower prey densities because their stomach capacity is very small and limited, while large larvae with greater stomach volumes can take advantage of higher plankton densities. From the standpoint of successful captures to obtain the maximum ration, smaller, younger larvae are actually much less efficient than larger.

This size effect on feeding ration over a range of prey densities has not been specifically examined for fish larvae before. Powers (1974) theoretically evaluated tha Ivlev relationship with laboratory feeding data for an amphipod, *Anisogammarus confervicolus*. He examined changing coefficients of proportionality (α) at constant maximum ration. The results showed that the asymptote is approached more quickly at higher α's, similar to the results noted in this research. Powers did not analyze maximum feeding ration as a function of animal size at changing α's. He did, however, state that animal size would probably have an effect since larger animals are better predators than smaller ones.

The initial sharp reduction in feeding times predicted by the model following hatching until a dry weight of 75 μg (Figure 6) was undoubtedly due to the increased ability of growing winter flounder larvae to capture prey. This is supported by Schumann (1965), who reported that larvae of Pacific sardine, *Sardinops sagax*, which were initially successful at feeding increased their searching ability and the probability of capturing a subsequent prey. The increase in predicted feeding times from 75- to 500-μg size was due to the exponential increase in metabolic rate for premetamorphosed larvae (Laurence 1975). The reduction in predicted feeding time from the initiation of metamorphosis until its completion (500–1,000 μg) was related to the decrease in absolute metabolism due to behavioral changes of metamorphosing winter flounder (Laurence 1975) and their greatly increased efficiency at capturing prey, which required less energy expenditure. The decrease in predicted feeding time with increase in prey concentration was due to the increased chance of prey encounter and capture. Zaika and Ostrovskaya (1972) also confirmed this for Baltic smelt and Pacific herring, *Clupea harengus pallasi*, larvae when they theoretically showed that the time spent searching for food decreased exponentially with an increase in food concentration.

Most larval fish have been reported as visual feeders (Houde 1973) and require daytime light intensities for optimum feeding (Blaxter 1969). In view of this, it is surprising that little research has been done on the relationship of feeding parameters and available time for feeding. Ivlev (1961b) combining field and laboratory data for

Atlantic herring, *C. harengus,* from the Gulf of Finland reported that, at observed plankton concentrations in the field, the calculated time of feeding was 15 h. This coincided exactly with the length of day. Laurence (1971a), working with the stipulation of a 14-h feeding period for largemouth bass larvae, found that prey concentrations of 7.0 cal/liter (400 organisms/liter) were limiting. The results of this research show that simulated critical prey densities, below which winter flounder larvae do not have enough daylight hours for feeding to meet growth and metabolic energy requirements, actually vary with age and stage of development (Figure 7). The critical densities range from a high of 5.7 (0.8 nauplius/ml) to a low of 2.1 cal/liter (0.3 nauplius/ml) when feeding behavior has been established but before growth and metabolic demands are high. Critical density then increases until initiation of metamorphosis when it remains fairly constant around 4.5 cal/liter (0.6 nauplius/ml). Results such as these have not been quantitatively reported in the literature before. Most previous laboratory studies for a variety of species delineate constant critical prey densities for the larval period usually in the range 0.1–1.0 organism/ml (Kramer and Zweifel 1970; O'Connell and Raymond 1970; Saksena and Houde 1972; Laurence 1974; Houde 1975), although Rosenthal and Hempel (1970) reported that prey densities for optimum feeding (not critical densities) for larval Atlantic herring were higher for younger than older larvae.

The critical prey densities for larval survival of approximately 0.5 organism/ml noted in this and the other cited laboratory research are somewhat disparate with densities described from field data. Lisivnenko (1961) noted that larval Baltic herring were much less abundant in years when prey abundance was <0.01 organism/ml. Sysoeva and Degtereva (1965) reported that the minimum abundance of *Calanus finmarchicus,* when the intensity of feeding of cod, *Gadus morhua,* larvae decreased, was from 0.01 to 0.005/ml and that a concentration of 0.02/ml provided sufficient food for survival. It is my opinion that the results reported for laboratory studies may be more accurate than the field study data presented thus far. The laboratory studies represent highly controlled experiments with accurate counts of prey organisms. On the other hand, the field studies give estimates of prey abundance which represent average densities over linear or oblique sampling distances. Planktonic prey organisms have contagious distributions and larvae may well be associated with "patches" of prey that are more densely concentrated than indicated by plankton net tows (Wyatt 1973). Many larval fish researchers feel that density dependent mechanisms control larval survival (Cushing and Harris 1973), and the concept of contagious distributions in which larvae and prey are associated in "clumps" that may or may not be associated and occupying the same area is one of the most logical ways to explain the fluctuations noted for natural larval mortality. Also, field zooplankton sampling designs rarely use nets with mesh smaller than 200 μm. Most of the significant food organisms utilized by larval fishes especially in the early stages are <200 μm in smallest dimension (Houde 1973) and would be lost in field sample estimates. Use of the plankton pump may prove to be more accurate in locating patches of zooplankton and sampling the size organisms that larval fish consume. Recently, Heinle and Flemmer (1975), using a moving plankton pump, reported concentrations of nauplii of *Eurytemora affinis* in the Chesapeake Bay area as high as 2.8/ml with concentrations of 1.0–1.8/ml not at all uncommon. These concentrations are more than adequate for good growth and survival of winter flounder larvae and many other larval species.

The initial, predicted decrease in metabolic energy expended (Figure 8) during the period of feeding initiation and shortly after (10–30 μg dry weight) is undoubtedly explained by the increased feeding success with experience by first feeding larvae. First feeding individuals have a lower success ratio of captures and have to expend more energy in searching for prey than older and more accomplished feeders. This success or fail period is critical to eventual survival and is relatively short in duration for winter flounder, occurring during the first 8 days after feeding begins at 8°C. The increase in metabolic energy expended from 30- to 500-μg dry weight after successful feeding establishment is due to normal increases in energy demand for all processes with rapid increases in size usually seen in larval fishes. The leveling off of metabolic energy demand during the metamorphosis period (500–1,000 μg dry weight) may be unique to flatfishes due to marked morphological and behavioral changes (Laurence 1975) and increased predatory efficiency requiring less energy expenditure.

The decrease in metabolic energy expenditure with increasing prey concentration is logically

explained by the increased chance of successful feeding at higher plankton concentrations and concurrent decrease in energy expended to obtain prey. Warren and Davis (1967) concurred with this type relationship, stating that the density of food determines an animal's energy cost in obtaining the food. Decreasing metabolism with increasing food concentration is contrary to reported laboratory studies using fish older than the larval stages. Paloheimo and Dickie (1966a) and Beamish and Dickie (1967), examining data from other researchers, concluded that higher average metabolic rates result at higher feeding rates. However, it may be presumptuous to assume this type relationship for fish larvae. Most older, nonplanktivorous feeding fishes, such as those referred to in the above citations, are satiation or periodic feeders. In fact, most of the experimental data cited above were for restricted daily diets at different levels. Larval fish, like the winter flounder, are active continuous feeders and the assumption in this model was continuous feeding at maintained prey densities. Older fish have more body reserves and can exist on maintenance rations to which they can adjust metabolically in contrast to larval fish which must feed continuously and are committed to growth or else die. In fact, the concept of maintenance probably is not relevant to larval fish feeding and energetics. So, it seems logical that fish larvae feeding continuously and committed to relatively high growth rates would optimize growth by reduced metabolic expenditure which would result from the increased contact and efficiency of capture at higher prey densities and resultant feeding levels. The research of Wyatt (1972) with plaice larvae tends to further support this concept. He noted that activity, which he attributed to food searching, decreased with increasing prey concentration.

The trends of nonassimilated energy over the range of weights and plankton concentrations in this research are similar to those for metabolic energy expenditure and food consumption (Figure 9). This is not surprising due to the interrelationships of these factors. The decrease in nonassimilated energy with increasing weight (10–30 μg) for first feeding larvae is apparently due to their initial inefficient digestion which improves with morphological development. Visual examination of food in the anterior portions of the digestive tracts of young larvae during the digestion rate studies indicated relatively intact nauplii. This has been observed for other larval fish species. Rosenthal and Hempel (1970) noted that the efficiency of digestion in Atlantic herring fed *Artemia* nauplii was very low compared with older larvae. Morphological development of the alimentary tract during the larval stage was studied by Nishikawa (1975) who noted an increase in stomach size and extension of the digestive tract as a whole in relation to increasing standard length. He postulated that these morphological developments cause a rapid increase in the function of the organs during the larval period. The subsequent increase in nonassimilated energy with size of winter flounder larvae is merely proportional to the increased ration.

Daily food requirements of winter flounder larvae were initially higher for the period associated with first feeding (10–30 μg, first 2–3 wk after hatching, Figure 10). These short-term higher requirements were due to the inefficient manner in which newly feeding larvae captured prey and the associated, higher energy expenditure. Researchers have reported that young fish larvae are much less adept and successful at capturing prey than older larvae. Braum (1967) showed that freshwater whitefish larvae, *Coregonus wartmanni,* increased their successful captures from 3 to 21% during the first 16 days of feeding. Schumann (1965) noted an obvious increase in proficiency at capturing food with increased age of Pacific sardine larvae. The reasons for increased success with age are increased visual perception of food organisms and increased locomotor abilities with advancing development (Blaxter 1965; Rosenthal and Hempel 1970). The subsequent increase in required ration with larval size was the result of normal increased energy demand of growth and metabolism associated with larger sized larvae. An interesting fact is the decrease in rate of food requirement noted in metamorphosing larvae (500–1,000 μg). This may be associated with the previously mentioned decrease in routine metabolic rate peculiar to flatfish larvae and increased efficiency of prey capture during the metamorphosis period. Riley's (1966) results for another flatfish, the plaice, *Pleuronectes platessa,* substantiate this observation. He noted declining ingestion rates and rations during metamorphosis.

Conversion of the caloric values of daily food required into numbers of nauplii or older stages consumed (Figure 11) showed, of course, the same trends for food required. This conversion does,

however, give a different perspective in that it shows the actual numbers of organisms that winter flounder larvae require on a daily basis. The differences in numbers between nauplii and older stages reflect the differences in sizes providing equivalent caloric intake. Also, winter flounder larvae did not feed entirely on nauplii, but changed in part to larger stage copepods as they grew older. Size selection of prey by larval fishes has been shown to be a factor of mouth size which increases with increased larval size (Shelbourne 1965; Blaxter 1969; Detwyler and Houde 1970; Shirota 1970). The numbers of nauplii consumed per day ranged from 19 to 235 over the range of sizes and plankton densities. These values are similar to requirements for other larval species (Chiba 1961; Braum 1967; Rosenthal and Hempel 1970), although temperature, larval species and size, and food organisms can account for variable results.

Decrease in percent food eaten per day with body weight (Figure 13) is in accordance with results of other researchers and was due to the relative decrease in the rate of food intake compared with the growth rate with larval development. Pandian (1967) observed decreases in percent eaten per day with increases in body size of *Megalops cyprinoides* and *Ophiocephalus striatus,* as did Laurence (1971b) for larval largemouth bass and Stepien (1974) for larval sea bream.

The percentages of body weight consumed per day predicted in this research were high from over 300% at the smallest larval sizes and lowest prey concentration to 27–31% at the higher prey concentrations and largest larval sizes. Percent body weight eaten per day is typically much greater for larval and juvenile fishes as compared with adults since there is a much higher energy demand for growth purposes (Winburg 1956). Stepien (1974), in the only other known comparable research on marine larvae, also reported high percentages. His results for sea bream at 29°C were from 222.4% for 2-day hatched larvae to 79% for 7-day-old larvae. Sorokin and Panov (1965) reported 40–60% body weight eaten per day by larval freshwater bream.

The gross growth efficiencies recorded in this research increased rapidly with size for the smallest larvae (10–75 μg) and then increased at a decelerated rate for the remainder of the larval period to metamorphosis (Figure 14). Increased gross growth efficiency at greater body weights observed in my experiments is contrary to the results of research with older fishes. Parker and Larkin (1959) stated that within any growth stanza the gross efficiency must decline with increasing size, as a greater portion of the food must be used in maintenance. This may not be true for larval fishes, as their development is so rapid that a large portion of the energy derived from food intake is used in growth. It is my opinion that larval fishes could not exist on a maintenance ration. Rapid growth is a definite prerequisite for successful survival in the environment of larval fishes, and they must either consume food at high levels with resultant rapid growth or die. The ability of larvae to increase their feeding efficiency with increased size could also contribute to greater growth efficiency.

Divergent opinions have been expressed by researchers concerning the relationship between growth efficiency and feeding level or prey concentration. Paloheimo and Dickie (1966b) stated that growth efficiency declined with increasing ration. Warren and Davis (1967) showed that growth efficiency increased to two-thirds the maximum feeding level and then decreased. Finally, Davies (1964) demonstrated that efficiency of digestion and absorption of food by goldfish, *Carassius auratus,* was improved by increasing food input over a given weight range. He postulated that secretion of digestive fluids was stimulated by the effects of increased food. In all cases the studies and analyses were done with adult fishes. Winter flounder larvae increased their gross growth efficiencies with increased plankton density similar to Davies' results. However, the causative mechanism was most likely the increased efficiency of prey capture with increased prey encounter at higher densities with resultant metabolic savings for growth rather than increased secretion of digestive fluids. Growth efficiency is most likely a dynamic factor not subject to generalizations and dependent on life stage, type of feeding strategy, or prey type.

The range of values of growth efficiency for larval winter flounder on this research were from 5 to 33%, depending on larval size and plankton concentration. These values are similar to those for other young fishes (Ivlev 1939a; Sorokin and Panov 1965; Edwards et al. 1969; Laurence 1971a; Frame 1973; Stepien 1974).

The above discussions have revealed that there are interrelationships between the bioenergetic parameters simulated by the model and that the whole system works in a circular pathway to

maintain an energy balance in the larva's body. Energy expended at a given temperature promotes growth and results in a metabolism that produces activity, which in turn acts on the planktonic prey to provide an assimilated food intake that supplies energy for metabolism and growth. The whole process at a given temperature is in turn influenced by the size or age of larvae and the planktonic prey concentration. A good example which depicts the effect of larval age or size on these interrelationships and one which points to a definite "critical period" shortly after hatching around the period of feeding initiation is shown in Figure 15. In this figure the caloric expenditures for the important bioenergetic parameters over the range of weights from 10 to 50 μg are summed for all plankton concentrations. A definite divergence of energy away from growth to metabolism and nonassimilation with a resultant increased food requirement is shown during early life (10–30 μg). This period coincides with first feeding and is the time when larvae need to grow at a fast rate because of their small size, fragility, and vulnerability to predators. This identified "critical period" is caused by a number of factors and interrelationships including: 1) developmental factors of which reduced visual perception and locomotor (swimming) abilities in young larvae prevent efficient prey capture compared with older and better developed larvae; 2) less efficient conversion of food to flesh because of higher metabolic expenditure associated with more searching due to less efficient prey capture; 3) less efficient digestion in young larvae causing a smaller fraction of the food to be assimilated and be available for potential growth. As the larvae grow larger and older, especially during the metamorphosis period (50–1,000 μg), they become more efficient at converting food to growth. The slopes of the lines connecting the simulated values of the important bioenergetic components summed for all prey concentrations over the weight range of hatching to metamorphosis in Figure 16 show that the rate of growth accelerates more rapidly towards food consumption rate than metabolic and nonassimilation rates with increasing larval size after the critical period.

In addition to the critical period, plankton density is an important determinant of larval survival and, of course, interacts crucially during the critical period. The overall influence of prey density is shown in Figure 17 where the caloric expenditures of the important bioenergetic parameters simulated by the model are summed over all weights at each plankton concentration. It can easily be seen that low prey densities strongly affect the dispensation of energy available from food consumption in comparison with high densities. A greater portion of the energy intake is utilized for metabolism and is not assimilated

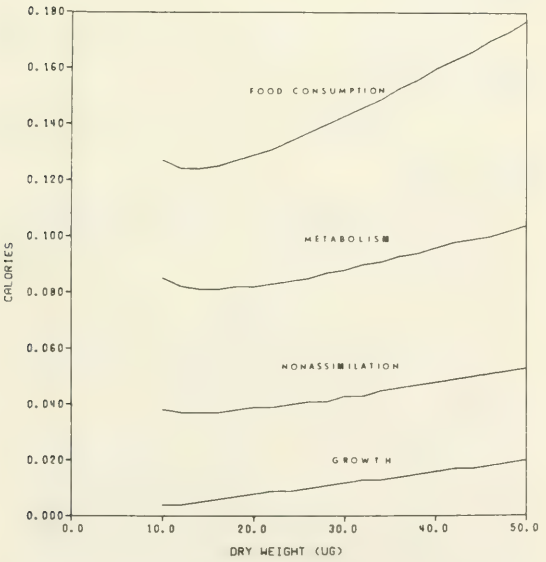

FIGURE 15.—Caloric energy expenditure for the major bioenergetic parameters of winter flounder larvae summed for all prey concentrations over the range of dry weights from 10 to 50 μg at 8°C.

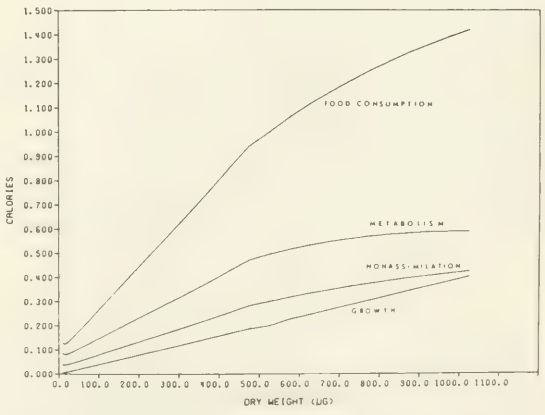

FIGURE 16.—Caloric energy expenditure for the major bioenergetic parameters of winter flounder larvae summed for all prey concentrations over the range of dry weights from hatching to metamorphosis at 8°C.

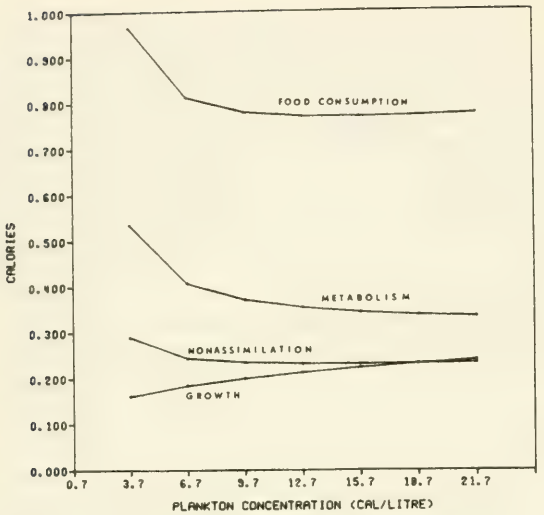

FIGURE 17.—Caloric energy expenditure for the major bioenergetic parameters at 8°C of winter flounder larvae summed for all dry weights from hatching to metamorphosis at different planktonic prey concentrations.

than is used for growth at lower prey densities. Also, the food requirements are higher at the lower densities which causes problems because food is harder to obtain at lower densities.

In conclusion, these experimental studies and model simulations demonstrate that there is strong evidence for a "critical period" of mortality in the larval stage of winter flounder and that planktonic prey density is one of the most important factors affecting survival during the larval stage. Additionally, the bioenergetic model developed presents a means to assess other trophic interactions in the marine, planktonic community. Larval fish are planktonic carnivores and the food requirements predicted by the model in combination with biomass estimates of larvae and prey and survival estimates of larvae can be used to predict the impact of larval grazing on their prey. This type of research is currently being pursued in continuing studies.

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DESCRIPTION OF LARVAL AND EARLY JUVENILE VERMILION SNAPPER, *RHOMBOPLITES AURORUBENS*[1]

WAYNE A. LAROCHE[2]

ABSTRACT

Larval and early juvenile development of vermilion snapper, *Rhomboplites aurorubens*, family Lutjanidae, is described and illustrated. Identification and description are based upon morphology, pigmentation, and meristics of 27 larval and 11 early juvenile specimens ranging from 4.0 to 14.2 mm standard length. All specimens were collected 65 km east of Sapelo Island, Ga., lat. 31°30'N, long. 80°30'W on 10 August 1972.

Larval and early juvenile vermilion snapper, *Rhomboplites aurorubens* (Cuvier), family Lutjanidae, are described from 27 larval and 11 small juvenile specimens collected at a station located approximately 65 km east of Sapelo Island, Ga., lat. 31°30'N, long. 80°30'W on 10 August 1972 (depth 22 m, surface temperature 26.7°C).

The genus *Rhomboplites* is monotypic and occurs only in the western Atlantic, from North Carolina and Bermuda to Rio de Janeiro, Brazil, including the Gulf of Mexico (Jordan and Evermann 1898; Hildebrand and Schroeder 1928; Hildebrand 1941; Anderson 1967; Böhlke and Chaplin 1968). Walker (1950) and Munro et al. (1973) reported *R. aurorubens* with mature ovaries during the cooler months, but Munro et al. (1973) suggested that some lutjanids may spawn throughout the year. I was unable to find any descriptions of lutjanid larvae. Small juveniles of the genera *Lutjanus* (Starck 1971; Heemstra 1974; Fahay 1975) and *Symphysanodon* (Fourmanoir 1973) have been illustrated.

METHODS

All specimens were collected by personnel aboard the U.S. National Marine Fisheries Service RV *Delaware II*. Ichthyoplankton was collected with a 60-cm diameter, 0.505-mm mesh, bongo net towed obliquely at 1.1 km/h (0.6 knot) from 20 m to the surface.

The specimens were stored in 3–5% buffered Formalin[3] after being removed from the sample (fixed in 10% buffered Formalin). Specimens were lightly stained with alizarin to facilitate measuring and counting body parts. One specimen (10.8 mm) was cleared and stained using the technique of Taylor (1967).

Illustrations were prepared using a camera lucida. Measurements were taken on the left side with an ocular micrometer. Measurements include:

Standard length (SL)—distance from tip of snout to posterior tip of notochord (before hypural formation) and tip of snout to posterior margin of hypurals (after hypural formation posterior to notochord tip).

Head length—distance (horizontal) from tip of snout to cleithrum.

Snout to anus—distance from tip of snout to posterior margin of anal opening.

Body depth—vertical distance between dorsal and ventral surfaces, to the ventral tip of the cleithrum.

Eye diameter—maximum diameter of eye.

Spine and fin ray lengths—distance from point of entry of spine or ray into flesh to distal tip.

IDENTIFICATION

Identification of the series was based on counts of small juvenile specimens which had 24 myomeres; 7 branchiostegal rays; XII, 11 dorsal fin

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spines and rays; III, 8 anal fin spines and rays; 17–18 pectoral fin rays; I, 5 pelvic fin spine and rays; 9+8 principal caudal fin rays. Taxa listed by Bailey et al. (1970) were checked for the counts listed above. Only *R. aurorubens* was found to have the above counts (Jordan and Evermann 1898; Hildebrand and Schroeder 1928; Anderson 1967; Böhlke and Chaplin 1968; Miller and Jorgenson 1973) among fishes inhabiting western North Atlantic waters less than 200 m deep. Larvae were linked to the juvenile specimens by similarities of morphology and pigmentation.

Future identifications of small larvae based upon this paper should be made with care since larvae of other lutjanids have not been described.

DESCRIPTION OF LARVAE AND JUVENILES

Only large larval and small juvenile stages are described since egg, yolk-sac, and small post yolk-sac stages were not available. Larvae are defined as all forms between yolk-sac absorption and differentiation of the adult complements of spines and soft rays in the fins. Transformation from larva to juvenile is gradually completed between 8.3 and 10.9 mm.

Pigmentation

Head pigmentation increases through the larval period (Figures 1, 2) with the smallest larva (4.0 mm) showing least pigmentation (Figure 1A). Head pigmentation includes a large stellate melanophore centered over the posterior portion of the midbrain and another on the ventral surface anterior to the tips of the cleithra (Figures 1, 2). The large dorsal melanophore is present on all larval and juvenile specimens except one which has a melanophore over each hemisphere of the midbrain on either side of the point where the central melanophore would be expected. A small area of internal pigmentation is also present ventral to the juncture of the midbrain and hindbrain. As the larvae increase in size, smaller stellate melanophores develop on each hemisphere of the midbrain anterior to the large central melanophore.

By 4.8 mm, a melanophore appears posterior to the dorsal tip of the opercle and 2 or 3 melanophores appear on the body beneath the opercle anterior to the cleithrum. Additional melanophores are added to the area of internal pigmentation ventral to the juncture of midbrain and hindbrain (Figure 1B).

There is a gradual increase of pigmentation over the forebrain and midbrain until melanophores form a cap of pigment over those structures (Figure 2B, C). From 15 to 20 melanophores per forebrain hemisphere and from 60 to 80 melanophores per midbrain hemisphere make up the cap in larger juvenile specimens (>10.0 mm). Three to five small melanophores appear at 9.0 mm scattered along the dorsal surface of the snout. On juveniles >10.0 mm, 8–12 small melanophores are scattered on the anterior portions of upper and lower lips.

Preanal body pigmentation includes dense peritoneal pigment which spreads ventrally in bands along the dorsolateral surface of the coelomic wall. The banding results from variations in size and spacing of discrete melanophores. Peritoneal pigmentation appears less distinct on largest juveniles due to an increase in overlying musculature. A pronounced melanophore occurs on the ventral surface anterior to the anus on all specimens <5.1 mm, and occasionally on those 5.1–6.3 mm, but is absent on individuals >6.3 mm.

A large stellate melanophore is present (on all specimens examined) internally on myomere 15, 16, or 17 above the posterior end of the anal fin near the ventral body margin (Figures 1A, B; 2A–C). Three to seven smaller melanophores develop anteroventrally to this spot along the bases of anal fin rays, appearing first on 4.7-mm larvae and occurring on all larger specimens (Figures 1C, 2). Posterior to the large internal melanophore, 1–4 melanophores occur on the ventral margin of specimens <7.0 mm. The number of melanophores present in this region is variable, tending to increase in number with body length, specimens >7.0 mm having 5–12.

A small melanophore appears on larvae 5.1–5.4 mm along the dorsal margin of myomere 21 or 22. Specimens >5.4 mm have 5–9 melanophores on the dorsal margin of the caudal peduncle (Figure 2B, C). At 4.9 mm, an internal melanophore appears dorsal to the point of notochord flexure and is present in all larger specimens examined (Figure 2A–C). An additional melanophore appeared anterior to this melanophore in two specimens, 8.7 and 10.5 mm long. Specimens with all principal caudal rays developed have 1–6 melanophores near the bases of the rays, usually on the lower 8 principal rays (Figure 2).

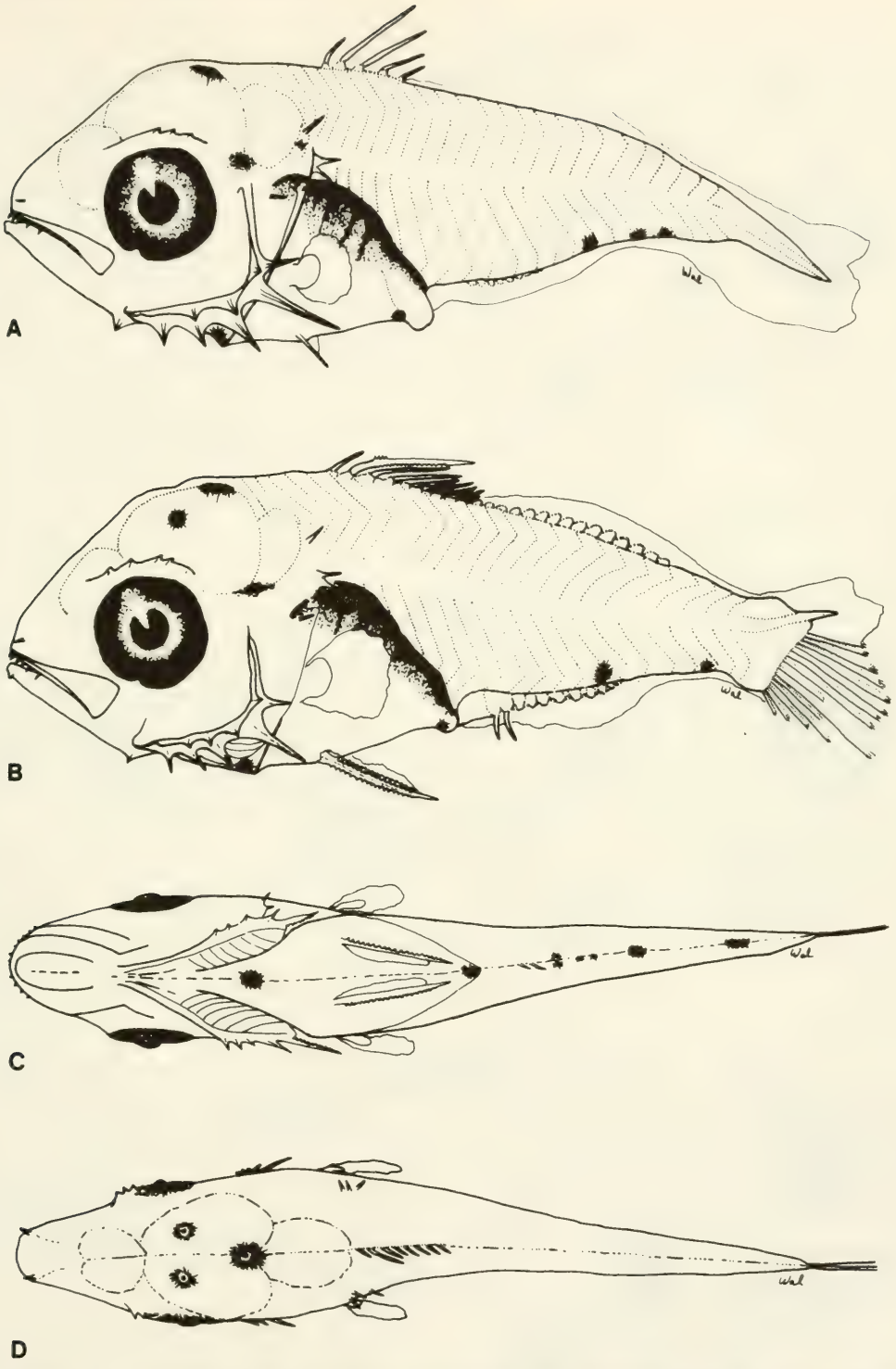

FIGURE 1.—Developmental stages of *Rhomboplites aurorubens:* A. 4.0-mm larva; B. 4.7-mm larva; C. 4.7-mm larva, ventral view; D. 4.7-mm larva, dorsal view.

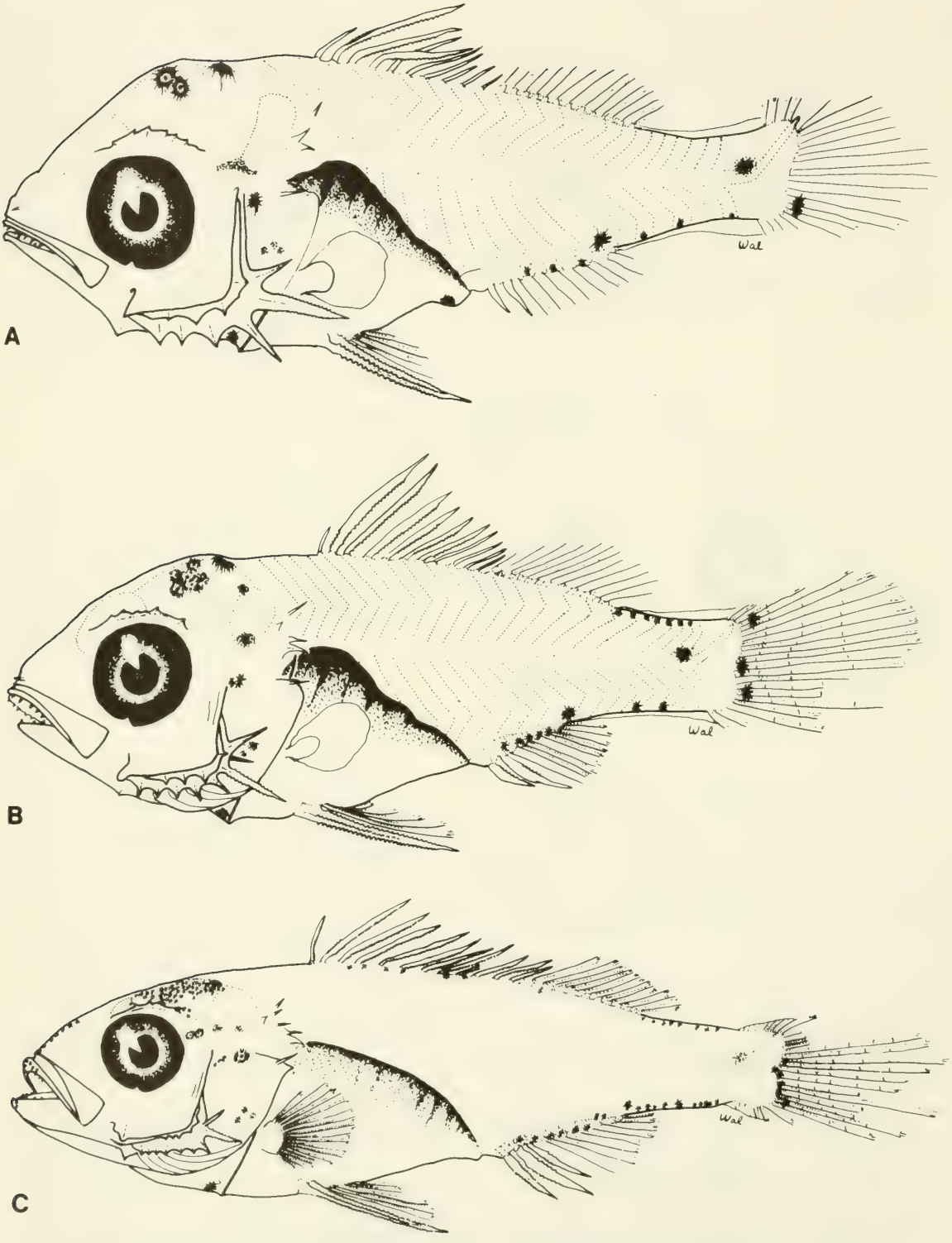

FIGURE 2.—Developmental stages of *Rhomboplites aurorubens:* A. 5.1-mm larva; B. 6.9-mm larva; C. 14.2-mm juvenile.

Fin Formation

Dorsal and pelvic fin formation begins by 4.0 mm (Figure 1A). Other fin development initiates in the following sequence: caudal, anal, and pectoral. The pelvic fins are first to complete development, while the dorsal fin is last.

Dorsal Fin

The anterior five dorsal spines are present on the smallest larva (4.0 mm) with an undifferentiated fin fold continuing to the caudal region (Figure 1A). The fin develops from anterior to posterior. At 4.8 mm, the adult number of dorsal fin elements appears with the posterior 1–3 spinous dorsal elements represented by soft rays.

Development of the dorsal fin occurs rapidly between 4.0 and 4.8 mm. After the adult number of fin-ray elements (23) appears, development towards the final adult dorsal fin complement (XII, 11) proceeds slowly as spines form from soft rays immediately posterior to the posteriormost spine. Dorsal spine development is similar to that described by Mansueti (1958) for anal spine development in *Roccus saxatilis*.

The dorsal fin is the last fin to attain the adult complement of spines and rays. Attainment of full dorsal fin complement between 8.3 and 10.9 mm marks the division between larval and juvenile stages.

The fourth dorsal spine is longest in adult *Rhomboplites aurorubens* (Jordan and Evermann 1898). The second dorsal spine is longest in all specimens of my series except the largest juvenile (14.2 mm) in which the third spine is longest (Figure 2C). The longest dorsal spine is longer than the longest dorsal soft ray throughout the series.

Dorsal spines are V-shaped in cross section, with the V open posteriorly. The two posterior edges are serrated nearly to the tip, which is sharp and oval in cross section. On larger spines the anterior edge is sometimes serrate for a short distance above the base (Figures 1B, 2B, C). Specimens between 4.8 and 9.0 mm have 29–40 serrations along each posterior edge of the second dorsal spine; larger specimens have 42–45 serrations.

Pelvic Fins

Pelvic fin spines and fin folds compose the pelvic fins of the 4.0-mm larva (Figure 1A). The pelvic fin attains the adult complement of I spine and 5 rays between 4.7 and 4.8 mm. The pelvic spine is long and serrate, extending slightly beyond the anus (24% SL) at its longest (about time of dorsal fin completion). Small specimens have spines which are V-shaped in cross section with serrations along all three edges. Specimens >4.5 mm have a double row of serrations along the leading edge of the spines creating an almost trapezoidal appearance in cross section (Figure 2).

Caudal Fin

The adult caudal fin has 17 principal and 19–21 procurrent rays (Miller and Jorgenson 1973). Principal rays are divided into two groups with 9 rays above and 8 rays below the midline of the body.

Notochord flexure occurs between 4.8 and 4.9 mm (Table 1). Flexure probably results in a slight decrease in standard length because the angle of the flexed notochord shortens the horizontal distance from snout tip to end of notochord. As a result of flexure and individual variation in rate of development, larvae of equal length may be at various stages of development (Table 1).

The caudal fin starts to form at the beginning of notochord flexure, about 4.7 mm. Fifteen or sixteen principal rays form simultaneously, slightly below and ventral to the posteroventral margin of the notochord. As the notochord flexes, these rays become elevated into the terminal position. The remaining rays are added dorsally and ventrally until the adult principal ray number is attained at about 4.8 mm (Figures 1B, 2A).

Anal Fin

The adult fin ray complement for vermilion snappers is III spines and 8 soft rays. Initial anal fin formation occurs at 4.7 mm. Embryonic fin rays (actinotrichia) are visible on 4.8-mm larvae. True soft rays (lepidotrichia) begin to form by 4.9 mm. The fin ray count remains II, 8 until about 5.4 mm and then becomes II, 9 (Table 1). The posteriormost ray forms last. The adult complement (III, 8) appears at about 8.3 mm as the anteriormost soft ray transforms into a spine. Each spine becomes serrate along its posterior edge, larger spines having a few serrations along the base of the anterior edge. The second anal spine is longest throughout the series studied, but in adults the third spine is longer.

TABLE 1.—Development of meristic characters of larval and small juvenile vermilion snapper, *Rhomboplites aurorubens*.

SL (mm)	Principal caudal fin rays		Dorsal fin		Anal fin		Pectoral fin rays	Pelvic fin		Notochord flexure
	Upper	Lower	Spines	Rays	Spines	Rays		Spines	Rays	
4.00			V					I		straight
4.13			VI					I		straight
4.67	8	7	VIII					I		straight
4.80	8	8	IX		II	8		I	5	flexed
4.80	9	8	XI	12	II	7		I	5	straight
4.80	9	8	X	13	II	8		I	5	flexed
4.87	9	8	X	13	II	8		I	5	flexed
4.93	9	8	X	13	II	8		I	5	flexed
4.93	9	8	X	13	II	8		I	5	straight
5.07	9	8	VIII	15	II	8		I	5	flexed
5.07	9	8	X	13	II	8		I	5	flexed
5.07	9	8	IX	14	II	8		I	5	flexed
5.07	9	8	IX	14	II	8		I	5	flexed
5.13	9	8	XI	12	II	8		I	5	flexed
5.27	9	8	X	13	II	8		I	5	flexed
5.40	9	8	X	13	II	9		I	5	flexed
5.46	9	8	XI	12	II	9		I	5	flexed
5.46	9	8	X	13	II	9		I	5	flexed
6.06	9	8	X	13	II	9		I	5	flexed
6.13	9	8	XI	12	II	9		I	5	flexed
6.26	9	8	XI	12	II	9		I	5	flexed
6.33	9	8	XI	12	II	9		I	5	flexed
6.40	9	8	XI	12	II	9		I	5	flexed
6.53	9	8	XI	12	II	9		I	5	flexed
6.53	9	8	XI	12	II	9		I	5	flexed
6.53	9	8	XI	12	II	9		I	5	flexed
6.93	9	8	XI	12	II	9	16	I	5	flexed
7.80	9	8	XI	—	II	9	16	I	5	flexed
8.26	9	8	XII	11	III	8	16	I	5	flexed
8.60	9	8	XI	12	III	8	17	I	5	flexed
8.66	9	8	XII	11	III	8	17	I	5	flexed
9.00	9	8	XI	12	III	8	17	I	5	flexed
10.00	9	8	XI	12	III	8	17	I	5	flexed
10.53	9	8	XII	11	III	8	17	I	5	flexed
10.80	9	8	XII	11	III	8	17	I	5	flexed
10.93	9	8	XI	12	III	8	18	I	5	flexed
11.20	9	8	XII	11	III	8	17	I	5	flexed
14.20	9	8	XII	11	III	8	17	I	5	flexed

Pectoral Fins

The pectoral fins are the last to begin development, embryonic rays becoming visible at about 4.9 mm. Ray formation proceeds from dorsal to ventral. True rays begin to form at about 6.9 mm, the adult complement, 17–18 rays, appearing by 8.6 mm.

Pectoral fin rays were frayed and broken on many specimens (including the specimen in Figure 2C). Longest pectoral fin rays without obvious damage were 11.9–15.0% SL, having no obvious within range correlation with standard length.

Head

All larvae have one small spine projecting from the posterodorsal portion of the operculum. This spine is very small and difficult to locate on small specimens (Figures 1, 2).

The preopercle is armed with two rows of spines. The smaller spines are located proximally along the margin of the preopercular crest, and the larger spines occur distally along the preopercular margin (Figures 1, 2). Both preopercular crest and preopercular margin have an upper (ascending) and lower (horizontal) margin which form approximately right angles.

Specimens <5.0 mm have 2 or 3 spines along the lower margin and 1 spine on the upper margin of the preopercular crest. Larger specimens have 3 or 4 spines along the lower and 1 or 2 spines along the upper margins (Figures 1, 2). Spines increase in size towards the angle of the preopercular crest.

Three spines are present along the lower margin of the preopercular margin on specimens <4.0 mm, 4 spines on specimens 4.0–5.4 mm, 5 spines on specimens 5.4–9.0 mm, and 6 or 7 spines on specimens >9.0 mm. These spines increase in size towards the angle of the margin, larger spines being serrated on juvenile specimens. A large, stout, and serrate spine occurs at the preopercular angle in all specimens. Length of the angle spine was 6.5% SL on the smallest larva (4.0 mm). All

other specimens <8.0 mm had angle spines which were 10.1–14.6% SL, averaging 12.6%. Specimens >8.0 mm had angle spines which were 7.0–13.1% SL, averaging 9.7%. The largest juvenile (14.2 mm) had the smallest spine within this group (7.0%). One spine occurred on the upper margin of the preopercular margin of all specimens examined, with a smaller spine occasionally occurring between it and the angle spine (Figure 2B).

The posttemporal has 1 or 2 sharp spines projecting posterodorsally; the supracleithrum, 2–5 similar spines; the number of spines increasing with growth (Figures 1, 2). The supraocular crest has 2–7 serrations which increase in number with growth. A sharp projection which appears to be the anterior tip of the lachrymal bone projects anteriorly and slightly ventrally from each side of the snout on all specimens.

The eye is nearly circular and has a ventral cleft (Figures 1, 2).

Conical teeth are present on premaxillary and dentary of all specimens; vomerine and palatine teeth, on 14.2-mm specimen.

TABLE 2.—Measurements of body parts for larval and juvenile vermilion snapper, *Rhomboplites aurorubens*, in millimeters.

SL	Head length	Snout to anus	Depth	Eye diameter
4.00	1.53	2.00	1.32	0.52
4.13	1.69	2.23	1.42	0.60
4.67	1.90	2.67	1.65	0.62
4.80	1.92	2.53	1.65	0.68
4.80	2.13	2.93	1.85	0.75
4.80	1.92	2.80	1.82	0.68
4.87	2.03	2.73	1.75	0.70
4.93	2.20	2.97	1.88	0.75
4.93	1.87	2.93	1.88	0.70
5.07	2.11	2.93	1.82	0.72
5.07	2.13	2.93	1.84	0.72
5.07	2.26	3.13	1.82	—
5.07	2.00	2.87	1.85	0.70
5.13	2.13	3.00	1.88	0.72
5.27	2.21	3.20	1.85	—
5.40	2.26	3.20	2.00	0.75
5.46	2.21	3.27	1.92	0.78
5.46	2.24	3.20	2.08	0.80
6.06	2.52	3.60	2.08	0.85
6.13	2.55	3.53	2.18	0.85
6.26	2.52	3.73	2.30	0.90
6.33	2.65	3.77	2.20	0.90
6.40	2.55	3.87	2.28	0.91
6.53	2.83	4.00	2.38	0.92
6.53	2.68	4.13	2.20	0.90
6.53	2.65	4.00	2.50	0.88
6.93	2.78	4.33	2.40	0.95
7.80	3.12	5.06	2.60	1.05
8.26	3.27	5.33	2.67	1.12
8.60	3.07	5.27	2.93	1.15
8.66	3.33	5.47	2.93	1.12
9.00	3.40	5.60	2.93	1.12
10.00	3.53	6.13	3.20	1.30
10.53	3.73	6.73	3.47	1.35
10.93	4.00	6.73	3.47	1.35
11.20	3.93	7.00	3.53	1.40
14.20	4.93	8.46	4.00	1.48

Body Growth

Measurements of body parts is presented in Table 2. The growth of various body parts as related to standard length is described by linear regression analysis using Bartlett's three-group method for Model II regression (Sokal and Rohlf 1969). Statistics for regressions of head length, depth of body, snout to anus distance, and eye diameter versus standard length are presented in Table 3. Correlation coefficients are greater than 0.97 for all relationships.

TABLE 3.—Statistics describing regressions of body measurements versus standard length for larval and small juvenile vermilion snapper, *Rhomboplites aurorubens*. The x variable is standard length in all cases.[1]

Variable y	Size range (mm)	x	y	N	b	a	$S_{y \cdot x}$	r
Head length	4.00–14.20	6.64	2.62	37	0.326	0.454	0.217	0.988
Body depth	4.00–14.20	6.64	2.28	37	0.285	0.388	0.198	0.986
Snout to anus	4.00–14.20	6.64	4.01	37	0.672	−0.450	0.185	0.995
Eye diameter	4.00–14.20	6.73	0.91	35	0.110	0.170	0.090	0.978

[1] $\bar{x}$ = mean value of x, $\bar{y}$ = mean value of y, N = number of specimens examined, b = rate of increase of y with respect to x, a = regression line intercept, $S_{y \cdot x}$ = standard deviation from the regression, r = correlation coefficient.

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SHORT-TERM THERMAL RESISTANCE OF ZOEAE OF 10 SPECIES OF CRABS FROM PUGET SOUND, WASHINGTON

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ABSTRACT

Zoeae of 10 crab species were subjected to tests that simulated thermal stress associated with steam-powered electric stations. Shortly after hatching, the unfed zoeae were subjected to conditions simulating passage through heat exchangers (held at elevated test temperatures for 20 min with an abrupt increase and decrease from ambient) or mixing with thermal plumes (held at test temperature 1 to 4 h with temperatures gradually rising and decreasing from ambient). All species used in tests were hatched from February to November and were naturally acclimated to ambient conditions of the littoral zone. Observations were made on the point in temperature that zoeae became torpid in heat exchanger tests and on the TL_{50} (maximum temperature–time that 50% or more of the subjects survived 48 h after testing).

In the heat exchanger tests, the most sensitive species, the Bering hermit crab, *Pagurus beringanus*, and the porcelain crab, *Petrolisthes eriomerus*, did not become torpid at 24°C; their torpid point and their TL_{50} were at 26°C. The economically important Dungeness crab, *Cancer magister*, did not become torpid at 28°C; its TL_{50} was at 30°C. The TL_{50} of other species ranged from 30° to 34°C.

The TL_{50} of zoeae given the thermal plume test ranged from 26° to 34°C for a 1-h exposure and 24° to 32°C for a 2- to 4-h exposure.

Thermal conditions in heat exchangers are postulated to be more critical to the survival of zoea than mixing with thermal plumes. The maximum temperature that should be permitted in heat exchangers to protect the most sensitive species studied is 24°C for the Puget Sound area.

Thermal resistance of marine organisms should be understood before seawater in a specific area is used for industrial cooling. In the State of Washington, for example, nuclear power plants are being planned for construction by municipalities and industries. These plants require large quantities of seawater to cool condensers of the steam turbine system; their waste hot water would be discharged back into the environment, along with toxic chemicals (Becker and Thatcher[2]). Organisms entrained into steam electric stations would be subjected to mechanical injury (Marcy 1973) from passage through such a system. Studies are needed to fully evaluate the impact of entrainment and the discharge of altered waste water on the associated life; temperature effects are considered here.

Some information is available on the thermal maximums and optimums of two species of Puget Sound crabs (Todd and Dehnel 1960; Reed 1969; Prentice 1971; Mayer[3,4]). These studies show the effects of long-term temperature increases but do not depict situations related to industrial use of seawater for cooling. Experiments reported here were designed to simulate the stress that zoeae would be exposed to in passing through heat exchangers of steam electric stations and in mixing with thermal plumes of the waste water released into the environment.

This study is one of a series describing the thermal resistance of selected species of planktonic organisms. The time-temperature combinations used are considered a measure of thermal resistance (Fry 1971) because they are probably beyond the environmental tolerance of the species used. This paper describes the elevated temperatures that cause immediate and imminent

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[2]Becker, C. D., and T. O. Thatcher (compilers). 1973. Toxicity of power plant chemicals to aquatic life. Battelle Pac. Northwest Lab., Richland, Wash., WASH-1249, U.S. AEC, misc. pagination.

[3]Mayer, D. L. 1973. Thermal tolerance of *Cancer magister* eggs. *In* Q. J. Stober and E. O. Salo (editors), Ecological studies of the proposed Kicket Island nuclear power site, p. 412–419. Univ. Wash., Coll. Fish., FRI-UW-7304.

[4]Mayer, D. L. 1973. Response of Dungeness crab in a thermal gradient. *In* Q. J. Stober and E. O. Salo (editors), Ecological studies of the proposed Kicket Island nuclear power site, p. 420–429. Univ. Wash., Coll. Fish., FRI-UW-7304.

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death and stress to the zoeae of four species of anomuran and six species of brachyuran crabs acclimatized to natural ambient conditions. These crabs constitute some of the more important types in the littoral zone and include species important in sport and commercial fisheries. Testing was done at the National Marine Fisheries Service facility at Mukilteo, Wash., from May to October 1971 and in February 1972.

MATERIALS AND METHODS

Ovigerous crabs were collected from the mid-Puget Sound areas of Possession Sound, Poverty Bay, and at Alki Point. Graceful crab, *Cancer gracilis*, Dungeness crab, *C. magister*, and kelp crab, *Pugettia producta*, were collected subtidally; other species were taken on beaches during low tides. The messmate crab, *Pinnixa littoralis*, was collected inside horse clam, *Tresus capax*, that had been excavated. Most of the experimental species were ovigerous in May and June; the mud flat crab, *Hemigrapsus oregonensis*, black clawed crab, *Lophopanopeus bellus*, and porcelain crab, *Petrolisthes eriomerus*, had ovigerous individuals to August. *Pugettia producta* were ovigerous July to November.

Ovigerous crabs and pre- and posttest zoeae were held in aquaria receiving running seawater of temperatures ranging from 8.2° to 23.5°C (Table 1); salinity ranged from 24.1 to 28.3‰; and dissolved oxygen ranged from 5.6 to 9.0 ppm. Laboratory water was sometimes 3°C higher than ambient temperatures at the surface in the afternoon on sunny days in July and August because of heating of the water supply pipe. Other than this, the ambient water temperatures of the Mukilteo area were similar to that expected of central Puget Sound locations (Wennekens 1959).

TABLE 1.—Temperature of Mukilteo, Wash., laboratory seawater summarized by 10-day periods in 1972.

Month	Water temperature (°C)		
	Average		
	Low	High	Range
May	9.3	10.0	8.2–10.7
	9.9	10.4	9.1–11.1
	9.5	11.4	8.8–12.7
June	10.4	12.2	10.0–13.3
	10.4	12.7	9.7–14.3
	10.8	13.5	10.4–14.3
July	11.0	13.1	10.4–14.0
	—	—	—
	12.3	16.4	11.3–18.2
August	12.9	16.4	11.3–18.2
	16.6	20.7	13.5–23.5
	15.7	18.6	13.0–23.0
September	13.2	14.9	12.6–15.6
	12.9	15.5	12.5–16.8
	13.7	15.9	12.5–16.8

Test facilities consisted of floating holding boxes for test groups of zoeae and 5-liter battery jars for maintaining water baths of a controlled temperature. Holding boxes were 2.5 cm^3, with two screened sides having 0.110-mm apertures, attached to Styrofoam[5] for floatation. Battery jars received 3 liters of seawater immediately before testing. Temperatures were maintained within ±0.5°C of the test temperatures during experiments. Continuous aeration insured mixing and oxygenation.

Zoeae generally hatched within a week after their parents were collected, but some parents were held a month before hatching occurred. When the zoeae hatched (hatching of all ova of a parent occurred within about 12 h), 10 were counted into each of the holding boxes within 24 h of hatching and remained there, unfed, to the termination of an experiment. Zoeae used as controls were held at the temperature of laboratory water, and others were given two types of thermal tests.

To simulate passage through heat exchangers, holding boxes containing 10 zoeae were removed from water of ambient temperature and placed directly into battery jars having water of an elevated temperature ranging from 24° to 38°C by 2°C increments (Table 2). The zoeae remained at the elevated temperature for 20 min and were then placed into water of ambient temperature. Actual temperature change within the holding boxes was delayed. On the average, the increase from ambient to midway to the test level occurred in 5 s. Temperatures were within 1°C of the test level in 2 min. Decreases from test temperatures to ambient occurred in about 1½ min. Activity of zoeae was noted before, during, and after testing.

To simulate conditions encountered in thermal plumes, zoeae in holding boxes were placed in water of ambient temperature in the battery jar. The temperature of the water was then elevated to a test temperature ranging from 24° to 36°C by 2°C increments (Table 2) over a 30-min period. Specific groups of zoeae were held at specific test temperatures for durations of 1, 2, or 4 h. After this, the temperature was gradually decreased to ambient level over a 20-min period, and the

[5]Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Percentage survival of first stage zoeae 48 h after testing of 10 species of crabs subjected to a range of temperatures at four durations (percentages are from combined data of two or more tests). Increases to and decreases from a test temperature were rapid for the 20-min test (heat exchanger test) and gradual for the longer durations of exposure (thermal plume test).

Species	Minutes held at test temperature	Date at end of test	No. of parents	Control		No. zoeae tested	Survival at different water temperatures (°C)							
				No. zoeae	Percent survival		24	26	28	30	32	34	36	38
										Percentage				
Anomuran:														
Bering hermit crab,	20	6/20	2	60	53	30	80	[1]*55*	47	0	0	—	—	—
Pagurus beringanus	60	7/28					55	*73*	37	10	0	—	—	—
	120						*50*	30	0	17	0	—	—	—
	240						*65*	37	3	0	0	—	—	—
Granular hermit crab,	20	6/25	3	90	92	30	—	87	83	*70*	0	0	—	—
Pagurus granosimanus	60	6/27					—	93	80	*77*	0	0	—	—
	120	7/2					—	90	90	*53*	0	0	—	—
	240						—	90	*83*	23	0	0	—	—
Hairy hermit crab,	20	6/5	3	80	93	10-30	—	80	80	*53*	10	7	0	—
Pagurus hirsutiusculus	60	6/13					—	100	77	*85*	37	0	0	—
	120	6/23					—	*100*	80	*80*	30	0	—	—
	240						—	*80*	83	*65*	7	0	0	—
Porcelain crab,	20	6/23	3	40	83	10-30	—	45	30	0	0	—	—	—
Petrolisthes eriomerus	60	6/25					—	70	*50*	0	0	—	—	—
	120	7/2					—	*100*	0	0	0	—	—	—
	240						—	*80*	0	0	0	—	—	—
Brachyuran:														
Black clawed crab,	20	6/16	3	100	89	40	100	98	90	95	*63*	13	0	—
Lophopanopeus bellus	60	6/23					100	98	98	*85*	5	3	—	—
	120	9/16					90	100	98	*75*	8	0	—	—
	240						80	98	83	*55*	0	3	—	—
Dungeness crab,	20	6/7	4	60	93	50	100	90	80	*78*	14	0	—	—
Cancer magister	60	6/9					100	94	*74*	18	6	0	—	—
	120	6/28					100	96	*90*	0	0	0	—	—
	240	2/29/72					100	94	*62*	2	0	0	—	—
Graceful crab,	20	7/16	2	60	95	40	88	90	90	*88*	23	0	—	—
Cancer gracilis	60	7/18					93	90	*90*	25	0	0	—	—
	120						90	83	*93*	3	0	0	—	—
	240						93	85	*80*	0	0	0	—	—
Kelp crab,	20	9/2	2	80	100	40	—	100	100	100	*90*	10	0	—
Pugettia producta	60	10/15					—	98	100	98	*88*	0	0	—
	120						—	98	90	*93*	13	0	0	—
	240						—	95	*95*	30	0	0	0	—
Messmate crab,	20	7/30	2	80	95	40	90	83	85	*83*	25	0	—	—
Pinnixa littoralis	60	8/4					95	98	88	*60*	3	0	—	—
	120						83	85	*95*	30	0	0	—	—
	240						93	93	*63*	13	0	0	—	—
Mud flat crab,	20	6/13	5	130	98	20-50	—	100	100	100	92	*52*	0	0
Hemigrapsus oregonensis	60	6/18					—	97	98	96	94	*54*	10	—
	120	7/2					—	100	100	100	*100*	46	0	—
	240	7/8					—	100	90	100	*98*	48	0	—
		8/28												

[1]Italic denotes the TL_{50}.

holding boxes containing zoeae were replaced in aquaria with running seawater.

The numbers of replicate tests made at a temperature for a test varied because of numbers of ovigerous crabs available and numbers of zoeae resulting from a hatching. The offspring from at least two parent crabs of a species were used (Table 2). Some species were tested at intervals over a 2- to 3-mo period to indicate seasonal acclimation effects. One test for *C. magister* was made in 1972; all other species were tested in 1971. Percentage survival of a species of crab for a given duration and temperature is the combined survival of two to five tests made for a species (Table 2).

Observations were made on the levels of activity, point of torpor, and the TL_{50} (maximum temperature–time combination survived by 50% or more of subjects 48 h after testing) to evaluate the effects of experimental conditions. A 48-h posttest observation duration was deemed appropriate for these tests as the zoeae were not fed and could have been affected by starvation although they readily survived to 72 h.

TEMPERATURE EFFECTS

Temperature–time combinations for a type of test that was critical to the survival of the zoeae of a species were indicated by survival of the controls and by experimental conditions affecting activity and survival of the test subjects.

Zoeae used as controls had survival rates ranging from 53 to 100% (Table 2). Guidelines set in the American Public Health Association (1971) state that losses of greater than 10% of control subjects invalidate an experiment. Control zoeae of the Bering hermit crab, *Pagurus beringanus*, with a survival of 53%, *L. bellus* with a survival of 89%, and *Petrolisthes eriomerus*, with a survival of 83% fall below this standard. Although the TL_{50}'s are invalid for these species, the point of torpor is valid as it demonstrates an immediate condition the zoeae lapse into with a given temperature stress.

Activity and survival of a species of zoeae decreased with increasing temperature and duration at an elevated test temperature (Table 2). In heat exchanger tests, zoeae experienced a rapid temperature change and were initially hyperactive, probably as a result of thermal shock (Kinne 1964). With time, zoeae at a temperature 4°C below the TL_{50} appeared normal. Those at 2°C below TL_{50} had reduced activity and had difficulty maintaining themselves off the bottom. Subjects placed in water at the TL_{50} temperature and above were initially hyperactive, but in 2 to 7 min became torpid and sank to the bottom. Heat exchanger test temperatures producing torpor were 26°C for *Pagurus beringanus* and *Petrolisthes eriomerus* and 30°C for most other test species; the maximum was 32°C for *L. bellus*, *Pugettia producta*, and *H. oregonensis*. After the zoeae were returned to ambient conditions, those tested at the TL_{50} temperature had not become active after 20 min.

Zoeae subjected to the heat exchanger tests generally had high survival to the point of the TL_{50} (Table 2). Thereafter, mortalities were complete at 2° to 4°C higher except in the case of the hairy hermit crab, *Pagurus hirsutiusculus*, where all died at 6°C above the TL_{50}. The minimal TL_{50} was at 28° and 30°C for most other crabs; it was at 32°C for *Pugettia producta* and *L. bellus* (Table 2). The most tolerant species was *H. oregonensis* with a TL_{50} at 34°C.

Zoeae subjected to the thermal plume tests had lower TL_{50}'s than those given the heat exchanger tests (Table 2). The TL_{50} of zoeae given the 60-min test was similar to or 2°C lower than those given the 20-min heat exchanger test; TL_{50}'s were at progressively lower temperatures for the 120- and 240-min tests. Mortalities were complete at 2° to 4°C above the TL_{50}. The least tolerant species were the *Cancer* crabs (Table 2) with TL_{50}'s at 28°C for the 60- and 240-min tests. TL_{50}'s were generally at 30°C for the other crabs for the three time durations they were tested. The species with the highest tolerance was *H. oregonensis* with a TL_{50} at 34°C for the 60-min test and at 32°C for the 120- and 240-min tests.

DISCUSSION

The situation postulated to be most critical to the survival of the planktonic zoeae is their passage through heat exchangers; zoeae will be entrained into heat exchanger systems but those encountering thermal plumes will probably only be exposed to lowering temperatures (Coutant 1970) at the periphery where turbulence occurs.

The maximum temperature limit that should occur in heat exchangers is best described as the one causing no adverse effects to the least resistant species—to be consistent with the protection of all species tested. Conditions that could be overtly recognized as affecting the survival of the zoeae were the degree of stress causing torpor and the TL_{50}. While the TL_{50} directly relates to death, torpor indicates a condition that could indirectly cause death. Torpid zoeae would have their feeding interrupted and they would not be able to evade predators until they recovered. Selective predation on zoeae subjected to a stress below that causing torpor could also be a factor of survival at sublethal temperature–time combinations. In fish, for example, Coutant (1973) experimentally observed that rainbow trout, *Salmo gairdneri*, predators selectively preyed on juvenile rainbow trout and chinook salmon, *Oncorhynchus tshawytscha*, that had been exposed to shock temperature treatments of durations below that required for the prey to lose equilibrium.

The maximum temperature that had no observable effect on the species studied was 24°C, as this was the greatest stress that did not cause *Pagurus beringanus* and *Petrolisthes eriomerus* to become torpid. The maximum for other species should be no greater than 28°C for *Cancer* and up to 30° to 32°C for the most resistant species.

A properly sited steam electric station should not discharge hot waste water in quantities or at locations where thermal plumes would retain their integrity over periods of 1 to 4 h. This could be a problem if Puget Sound waters were intensively used for cooling. TL_{50}'s for the zoea subjected to the 1- to 4-h thermal plume test

ranged from 28° to 32°C, except that *H. oregonensis* had a TL_{50} of 34°C for the 1-h test.

The maximum temperature increase in a steam electric station that will not cause mortality to the species studied can be estimated from the seawater temperature in Puget Sound and the maximum temperatures tolerated by zoeae. Surface temperatures of Puget Sound range from about 10°C in the spring when most zoeae hatch to 15°C or more in some locations in the summer (Wennekens 1959). Temperatures in heat exchangers can be increased 14°C in the spring and 9°C in the summer without causing direct or indirect mortalities to the least resistant species. Synergistic effects from the release of toxic chemicals and from mechanical damage may act to lower the thermal maximums tolerated.

Knowledge of the temperature tolerance of the zoeae studied provides a partial input into the assessment of the impact of a steam electric station using Puget Sound waters for cooling. Zoeae are generally a minor component of zooplankton within the depths of Puget Sound that would be subject to entrainment (Hebard 1956; Patten unpubl. data). Also, the volume of water entrained by a steam electric station would be small in comparison to that of Puget Sound. Therefore, if all entrained zoeae were destroyed in a steam electric station, the proportion lost may be of minor concern on the population level. Losses of zoeae from high temperature conditions may be more serious if a series of steam electric stations used Puget Sound waters for cooling. In this case, some conservation measures should be considered.

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A SIMPLIFICATION FOR THE STUDY OF FISH POPULATIONS BY CAPTURE DATA

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ABSTRACT

Expressions given by Rafail for estimating catchability are modified here to eliminate iteration, for better accuracy, and a large economy in calculations and time. The evaluation of catchability allows the estimation of other important parameters with the useful assumption of their variabilities according to seasons and recognized sections of a population.

The evaluation of some parameters of fish populations from capture data began at the start of the century (Edser 1908; Heincke 1913; Baranov 1918). Beverton and Holt (1957) derived an equation in two forms (equations (14.19) and (14.86)) for the estimation of catchability and natural mortality from catch and effort data for a whole series of years assuming identical survival rates and catchabilities for all ages in a given year, fishing effort varies from year to year, and negligible recruitment and migrations.

Paloheimo (1961) modified the iteration method by Beverton and Holt (1957) to a simpler one without iteration using the relationship $(1 - e^{-i})/i \approx e^{-0.5i}$ where i is the instantaneous total mortality.

Allen (1966) described three methods for estimating a population and one for recruitment by using data on annual age composition, number caught, effort to take a known part of the catch assuming a constant recruitment rate all over a year, equal catchability for the different age groups, and available comparisons between exploited and unexploited populations with equal natural mortality. Allen (1968) described a simplification of his method for computing recruitment rates.

Among the investigators who studied the variability of parameters of fish populations, Gulland (1964) described variations in catchability as cyclical, long-term trends due to amount of fishing and changes in abundance, diurnal changes due to feeding and light, temperature like severe winters, and sex. Paloheimo and Kohler (1968) concluded from their analysis of a cod population that catchability and natural mortality showed variations associated with age and years. Walker (1970) gave evidence of increased natural mortality with age due to senescence for cod.

Rafail (1974) recognized the probable great variability of parameters of fish populations and derived expressions for the evaluation of catchability, fishing mortality, natural mortality, and recruitment assuming their variability from one season to another and their constancy during the seasons as well as their variation from a recognized section of a population to another like age-groups and different sexes. His equations for the evaluation of catchability as the first parameter to be estimated require a number of iterations which may be relatively very large if recruitments exceed the sum of natural and fishing mortalities. Therefore, a computer is needed for accurate calculations and this is a disadvantage.

The present treatment transforms the equations given by Rafail (1974) to estimate catchability into forms that dispense with iterations and yield more accurate estimates.

SAMPLING PROCEDURE

A fish population with a certain initial size is distributed on a constant area and subjected to a sequence of sampling surveys which can be grouped into a number of groups. Each group of surveys must contain at least three sampling surveys. The parameters of the population are assumed to vary among the groups of surveys and remain constant within each group which represents a season with constant properties. The entire fishing fleet may be considered as sampling

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vessels whose catch data are to be collected adequately.

If the fleet is large, a part of the fleet is appointed as sampling vessels while the effective fishing effort of unappointed vessels should be estimated. The sampling surveys should follow one another with no intervening time periods within a group of surveys. The durations of the surveys may vary from one survey to another or kept constant if the total fishing effort varys from survey to survey. The total effort exerted on the population should vary from one survey to another.

ASSUMPTIONS

1. A fish population has a constant area of distribution and a constant uniform distribution of fishing relative to fish concentration so that the instantaneous fishing mortality is proportional to fishing effort.

2. The population is subjected to a sequence of n sampling surveys grouped into M groups representing M seasons with constant population parameters. The duration of the kth survey is denoted by T_k. The catchability or percentage of available fish captured by a standard unit of fishing effort during the kth survey is denoted by q_k.

3. The commercial and sampling vessels exert a constant fishing effort per unit time during the kth survey denoted by f_{kc} and f_{ks} respectively, so that the efforts exerted become

$$f_{ks} \cdot T_k = f'_{ks} \quad (1.1)$$
$$f_{kc} \cdot T_k = f'_{kc} \quad (1.2)$$
$$f_{ks} + f_{kc} = f_k \quad (1.3)$$
$$f'_{ks} + f'_{kc} = f'_k \quad (1.4)$$

where f'_{ks}, f'_{kc}, and f'_k represent the total fishing effort exerted by the sampling, commercial vessels, and the whole fleet, respectively, during the kth survey.

4. The instantaneous fishing mortalities per unit time by the sampling, commercial, and total fleet in the kth survey are denoted by F_{ks}, F_{kc}, and F_k, respectively. The instantaneous fishing mortalities during the kth survey (F'_{ks}, F'_{kc}, and F'_k) are evaluated as

$$F_{ks} \cdot T_k = F'_{ks} = q_k \cdot f'_{ks} \quad (1.5)$$
$$F_{kc} \cdot T_k = F'_{kc} = q_k \cdot f'_{kc} \quad (1.6)$$
$$F_k \cdot T_k = F'_k = q_k \cdot f'_k. \quad (1.7)$$

5. The fish population has an initial size denoted by N_0. The number of fish present at the start of the kth survey is N_{k0} while the number of fish present at the end of the kth survey or the start of the $(k+1)$th survey is $N_{(k+1)0}$.

6. The instantaneous natural mortality rate per unit time during the kth survey is M_k. The instantaneous natural mortality during the kth survey is

$$M_k \cdot T_k = M'_k. \quad (1.8)$$

7. The instantaneous recruitment rate per unit time during the kth survey relative to the number of fish present is R_k. The number of fish present at the end of the kth survey or the start of the $(k+1)$th survey when recruitment is acting solely is

$$\begin{aligned} N_{(k+1)0} &= N_{k0} \cdot \exp(R_k \cdot T_k) \\ &= N_{k0} \cdot \exp(R'_k), \end{aligned} \quad (1.9)$$

that is,

$$R_k \cdot T_k = R'_k, \quad (1.10)$$

where R'_k denotes the instantaneous recruitment rate during the kth survey.

8. The instantaneous rate of change of fish abundance per unit time during the kth survey relative to the number of fish present is "A_k" which is the "instantaneous abundance coefficient" so that

$$\begin{aligned} N_{(k+1)0} &= N_{k0} \cdot \exp(A_k \cdot T_k) \\ &= N_{k0} \cdot \exp(A'_k). \end{aligned} \quad (1.11)$$

In other words, $A_k \cdot T_k = A'_k$ and A'_k denotes the instantaneous change of abundance during the kth survey.

According to previous assumptions we have

$$A'_k = R'_k - M'_k - F'_k = (R_k - M_k - F_k)T_k \quad (1.12)$$

and

$$\begin{aligned} N_{(k+1)0} &= N_{k0} \cdot \exp(A'_k) \\ &= N_{k0} \cdot \exp(R'_k - M'_k - F'_k). \end{aligned} \quad (1.13)$$

9. If the sampling surveys $(k-1)$, k, and $(k+1)$ belong to the same season,

$$R_{k-1} = R_k = R_{k+1} = \bar{R}_k \quad (1.14)$$
$$M_{k-1} = M_k = M_{k+1} = \bar{M}_k \quad (1.15)$$

and

$$q_{k+1} - q_k = q_{k+1} - \bar{q}_k \qquad (1.16)$$

where $\bar{R}_k$, M_k, and $\bar{q}_k$ are constant parameters per unit time during the $(k-1)$th, kth, and $(k+1)$th sampling surveys which should belong to the same season.

$$\therefore \qquad \bar{R}_k - M_k = \bar{B}_k \text{ (a constant).} \qquad (1.17)$$

10. If $T_k = T_{k-1} = T_{k+1}$ and similar to Equations (1.8), (1.10), and according to (1.17), we get

$$\bar{M}_k T_k = \bar{M}'_k,\ \bar{R}_k T_k = \bar{R}'_k, \text{ and } \bar{B}_k T_k = \bar{B}'_k \qquad (1.18)$$

where $\bar{M}'_k$, $\bar{R}'_k$, and $\bar{B}'_k$ represent the instantaneous rates of natural mortality, recruitment, and the difference between them during single surveys (not per unit time) belonging to the same season when the durations of the surveys are made equal.

11. The number of fish captured by the sampling, commercial, and the total fleet during the kth survey are denoted by C_{ks}, C_{kc}, and C_k, respectively.

12. The catch per unit efforts during the kth survey obtained from sampling, commercial, and total fleet are respectively

$$(C/f')_{ks},\ (C/f')_{kc}, \text{ and } (C/f')_k$$

where f is primed (f') according to previous notations to designate exerted effort during a whole sampling survey and not per unit time.

13. The following expressions are used to obtain simpler mathematical equations:

$$(\exp(A'_k) - 1)/A'_k = a_k \qquad (1.19)$$

$$a_k^2/a_{k+1} \cdot a_{k-1} = a'_k \qquad (1.20)$$

$$(C/f')_k^2/(C/f')_{k+1} \cdot (C/f')_{k-1} = (C/f)'_k. \qquad (1.21)$$

A MODIFICATION FOR THE EXPRESSION ESTIMATING CATCHABILITY

Rafail (1974) developed an estimate for $\bar{q}_k$ according to his equation (4.16) briefly as follows when the whole fleet is engaged for sampling:

$$C_k = N_0 \cdot \exp\left(\sum_{j=1}^{k-1} A'_j\right) \cdot F'_k \cdot a_k \qquad (2.1)$$

and

$$C_{k+1} = N_0 \cdot \exp\left(\sum_{j=1}^{k} A'_j\right) \cdot F'_{k+1} \cdot a_{k+1} \qquad (2.2)$$

$$\therefore \qquad \frac{C_{k+1}}{C_k} = \exp(A'_k) \cdot \frac{a_{k+1}}{a_k} \cdot \frac{F'_{k+1}}{F'_k} \qquad (2.3)$$

and

$$\frac{C_k}{C_{k-1}} = \exp(A'_{k-1}) \cdot \frac{a_k}{a_{k-1}} \cdot \frac{F'_k}{F'_{k-1}} \qquad (2.4)$$

and

$$\frac{C_k^2}{C_{k-1} \cdot C_{k+1}} = \frac{\exp(A'_{k-1})}{\exp(A'_k)} \cdot \frac{a_k^2}{a_{k-1} \cdot a_{k+1}} \cdot \frac{F'^2_k}{F'_{k-1} \cdot F'_{k+1}}. \qquad (2.5)$$

According to Equations (1.7) and (1.16) we get

$$\frac{F'^2_k}{F'_{k-1} \cdot F'_{k+1}} = \frac{\bar{q}_k^2 \cdot f'^2_k}{\bar{q}_k^2 \cdot f'_{k-1} \cdot f'_{k+1}} = \frac{f'^2_k}{f'_{k-1} \cdot f'_{k+1}}. \qquad (2.6)$$

As we have $\dfrac{\exp(A'_{k-1})}{\exp(A'_k)} = \exp(A'_{k-1} - A'_k)$ and according to Equation (1.12), we get

$$\exp(A'_{k-1} - A'_k) = \exp\Big((R_{k-1} - M_{k-1} - F_{k-1})T_{k-1} - (R_k - M_k - F_k)T_k\Big).$$

Again according to Equations (1.14) and (1.15), as well as (1.7) and (1.16), we get

$$\exp(A'_{k-1} - A'_k) = \exp\Big((\bar{R}_k - \bar{M}_k)(T_{k-1} - T_k) - \bar{q}_k(f'_{k-1} - f'_k)\Big). \qquad (2.7)$$

From Equations (1.20), (2.5), (2.6), and (2.7) we get

$$\frac{C_k^2}{C_{k-1} \cdot C_{k+1}} = \exp\Big((\bar{R}_k - \bar{M}_k)(T_{k-1} - T_k) - \bar{q}_k(f'_{k-1} - f'_k)\Big) \cdot a'_k \cdot \frac{f'^2_k}{f'_{k-1} \cdot f'_{k+1}}.$$

Rearranging and according to assumption 12 we get

$$\frac{(C/f')_k^2}{(C/f')_{k-1} \cdot (C/f')_{k+1}} = \exp\Big((\bar{R}_k - \bar{M}_k)(T_{k-1} - T_k) - \bar{q}_k(f'_{k-1} - f'_k)\Big) \cdot a_k.$$

Using Equation (1.21), the above equation is transformed to

$$\bar{q}_k = \frac{\log_e(a'_k) + (\bar{R}_k - \bar{M}_k)(T_{k-1} - T_k) - \log_e(C/f)'_k}{f'_{k-1} - f'_k}. \quad (2.8)$$

If sampling surveys are arranged to have equal durations (or $T_{k-1} = T_k = T_{k+1}$), then Equation (2.8) reduces to

$$\bar{q}_k = \frac{\log_e(a'_k) - \log_e(C/f)'_k}{f'_{k-1} - f'_k}. \quad (2.9)$$

Equations (2.8) and (2.9) will be modified if a part of the commercial fleet is engaged with the sampling surveys so that $(C/f)'_k$ will be replaced by $(C/f)'_{ks}$, so that the last expression will be evaluated from the catch per unit effort of the sampling vessels "$(C/f')_{ks}$ of assumption 12," while all other items will remain the same.

Again it is important to note that the data of three successive surveys should be used to obtain a single q-estimate because in case of unsuccessive data the fraction $\exp(A'_{k-1})/\exp(A'_k)$ of Equation (2.5) will be biased and Equations (2.8) and (2.9) will not hold good.

Equations (2.8) and (2.9) can be used to estimate $\bar{q}_k$ by a number of iterations which is large when fish abundance is increasing and much fewer with decreasing abundance (Rafail 1974).

The modification of Equations (2.8) and (2.9) is based on the fact that a_k shown by Equation (1.19) can be evaluated as a function of A'_k. Paloheimo (1961) gave the following approximation:

$$a_k = \big(1 - \exp(-A')\big)/A' \approx \exp(-0.5A'). \quad (3.1)$$

Rafail (1974) has shown that when the instantaneous rate of change of fish abundance is negative, then a_k of Equation (1.19) can be represented as in Equation (3.1). In fact a_k is more precisely expressed as

$$a_k \approx \exp(\alpha_1 A'_k + \alpha_2 A'^2_k + \alpha_3 A'^3_k) \quad (3.2)$$

where α_1, α_2, and α_3 denote certain constants. A simpler and sufficient precise expression for a_k is fitted here as

$$a_k \approx \exp(\pm 0.5A'_k + 0.04A'^2_k). \quad (3.3)$$

Table 1 shows a comparison between the values of a_k calculated by the exact Equation (1.19) and those calculated by Equation (3.3).

TABLE 1.—A comparison between a_k-values calculated according to the exact Equations (1.19) and (3.3).

A'	$\exp(A')$	$a = (\exp(A') - 1)/A'$	$x = \pm 0.5A' + 0.04A'^2$	$a = \exp(x)$
−0.02	0.9802	0.9901	−0.01	0.9900
−0.10	0.9048	0.9516	−0.0496	0.9516
−0.20	0.8187	0.9063	−0.0984	0.9063
−0.50	0.6065	0.7869	−0.2400	0.7866
−1.00	0.3679	0.6321	−0.4600	0.6313
−2.00	0.1353	0.4323	−0.8400	0.4317
−2.25	0.1054	0.3976	−0.9225	0.3975
−2.50	0.0821	0.3672	−1.00	0.3679
−2.65	0.0707	0.3507	−1.0441	0.3520
−2.75	0.0639	0.3404	−1.0725	0.3421
−3.00	0.0498	0.3167	−1.14	0.3198
0.02	1.0202	1.0100	0.010016	1.0107
0.10	1.1053	1.0530	0.05040	1.0517
0.20	1.2215	1.1075	0.10160	1.1070
0.50	1.6486	1.2972	0.26000	1.2968
1.00	2.7184	1.7184	0.54000	1.7160
2.00	7.3890	3.1945	1.16000	3.1900
2.25	9.4877	3.7723	1.32750	3.7716
2.50	12.1828	4.4731	1.50000	4.4817
2.65	14.1544	4.9639	1.60590	4.9823
2.75	15.6428	5.3246	1.67750	5.3521
3.00	20.087	6.3623	1.86000	6.4237

Table 1 shows that Equation (3.3) can be used to calculate a_k with a maximum error less than 1% when A' lies between ±3.00, i.e., an error which is practically negligible. Again, the smaller the value of A' the smaller is the error so that when A' lies between ±2.5, the error is less than 0.2%, and Equation (3.3) can be considered as a highly precise expression in that range which is always encountered in fisheries studies. Equation (3.3) can be used to evaluate a'_k given by Equation (1.20) as

$$a'_k = \frac{\big(\exp(\alpha_1 A'_k + \alpha_2 A'^2_k)\big)^2}{\exp(\alpha_1 A'_{k-1} + \alpha_2 A'^2_{k-1}) \cdot \exp(\alpha_1 A'_{k+1} + \alpha_2 A'^2_{k+1})}$$

and

$$\log_e a'_k = \alpha_1(2A'_k - A'_{k-1} - A'_{k+1}) + \alpha_2(2A'^2_k - A'^2_{k-1} - A'^2_{k+1}). \quad (4.1)$$

According to Equations (1.12), (1.14), (1.15), and (1.16) we get

$$A'_k = (\bar{R}_k - \bar{M}_k)T_k - F'_k \quad (4.2)$$

$$\begin{aligned} \therefore 2A'_k - A'_{k-1} - A'_{k+1} &= 2T_k(\bar{R}_k - \bar{M}_k) - 2F'_k \\ &\quad - T_{k-1}(\bar{R}_k - \bar{M}_k) + F'_{k-1} \\ &\quad - T_{k+1}(\bar{R}_k - \bar{M}_k) + F'_{k+1} \\ &= (\bar{R}_k - \bar{M}_k)(2T_k - T_{k-1} - T_{k+1}) \\ &\quad - 2F'_k + F'_{k-1} + F'_{k+1} \end{aligned}$$

or

$$2A'_k - A'_{k\ 1} - A'_{k-1} = (\bar{R}_k - \bar{M}_k)(2T_k - T_{k\ 1} - T_{k+1}) - \bar{q}_k(2f'_k - f'_{k\ 1} - f'_{k+1}). \quad (4.3)$$

Denoting

$$\alpha_2(2A'^2_k - A'^2_{k\ 1} - A'^2_{k-1}) \quad (4.4)$$

of Equation (4.1) by $\phi A'$.

Equations (4.3) and (4.4) can be used to evaluate $\log_e a'_k$ given by Equation (4.1) as

$$\log_e a'_k = \alpha_1(\bar{R}_k - \bar{M}_k)(2T_k - T_{k\ 1} - T_{k-1}) - \alpha_1\bar{q}_k(2f'_k - f'_{k-1} - f'_{k+1}) + \phi A'. \quad (4.5)$$

Equation (4.5) can be inserted in Equation (2.8) to have another expression for $\bar{q}_k$ as follows:

$$\bar{q}_k(f'_{k\ 1} - f'_k) = \phi A' + \alpha_1(\bar{R}_k - \bar{M}_k)(2T_k - T_{k-1} - T_{k+1}) - \alpha_1\bar{q}_k(2f'_k - f'_{k-1} - f'_{k+1}) + (\bar{R}_k - \bar{M}_k)(T_{k\ 1} - T_k) - \log_e(C/f)'_k$$

or

$$\bar{q}_k(f'_{k-1} - f'_k + 2\alpha_1 f'_k - \alpha_1 f'_{k\ 1} - \alpha_1 f'_{k+1}) = \phi A' + [\bar{R}_k - \bar{M}_k][T_k(2\alpha_1 - 1) + T_{k-1}(1 - \alpha_1) - \alpha_1 T_{k+1}] - \log_e(C/f)'_k$$

or

$$\bar{q}_k = \frac{\phi A' + [\bar{R}_k - \bar{M}_k][T_k(2\alpha_1 - 1) + T_{k\ 1}(1 - \alpha_1) - \alpha_1 T_{k+1}] - \log_e(C/f)'_k}{f'_k(2\alpha_1 - 1) + f'_{k\ 1}(1 - \alpha_1) - \alpha_1 f'_{k+1}}. \quad (5.1)$$

According to Equation (3.3) we find that 0.5 is a very good estimate for α_1 which can be inserted in Equation (5.1) to obtain

$$\bar{q}_k = \frac{\phi A' + 0.5(\bar{R}_k - \bar{M}_k)(T_{k\ 1} - T_{k+1}) - \log_e(C/f)'_k}{0.5(f'_{k\ 1} - f'_{k+1})}. \quad (5.2)$$

If sampling surveys are carried out during equal time intervals, i.e., $T_{k-1} = T_k = T_{k+1}$; Equation (5.2) becomes

$$\bar{q}_k = \frac{\phi A' - \log_e(C/f)'_k}{0.5(f'_{k-1} - f'_{k+1})}. \quad (5.3)$$

Equation (3.3) shows that α_2 is estimated at 0.04 so that $\phi A'$ becomes according to Equation (4.4) as

$$\phi A' = 0.04(2A'^2_k - A'^2_{k\ 1} - A'^2_{k-1}). \quad (5.4)$$

The correction term $\phi A'$ given in Equation (5.4) can be put in another form by the inspection of the term A' shown by Equation (4.2)

$$A'_k = (\bar{R}_k - \bar{M}_k)T_k - F'_k.$$

The parameters $\bar{R}_k$ and $\bar{M}_k$ are supposed to be constant during any group of sampling surveys according to assumption 9, and Equation (1.17) we have

$$\bar{R}_k - \bar{M}_k = \bar{B}_k \quad \text{a constant}$$

$$\therefore \quad A'_k = \bar{B}_k T_k - F'_k \quad (5.5)$$

and

$$A'^2_k = \bar{B}_k{}^2 T_k^2 - 2\bar{B}_k T_k F'_k + F'^2_k \quad (5.6)$$

and $\phi A'$ of Equation (5.4) becomes

$$\phi A' = 0.04(\bar{R}_k - \bar{M}_k)^2(2T_k{}^2 - T_{k\ 1}^2 - T_{k-1}^2) - 0.08(\bar{R}_k - \bar{M}_k)(2F'_k T_k - F'_{k-1}T_{k-1} - F'_{k+1}T_{k+1}) + 0.04(2F'^2_k - F'^2_{k-1} - F'^2_{k+1}). \quad (5.7)$$

If $T_k = T_{k-1} = T_{k+1}$ and according to Equation (1.18) we have

$$\bar{M}_k T_k = \bar{M}'_k \text{ and } \bar{R}_k T_k = \bar{R}'_k$$

$$\therefore \phi A' = -0.08(\bar{R}'_k - \bar{M}'_k)(2F'_k - F'_{k-1} - F'_{k+1}) + 0.04(2F'^2_k - F'^2_{k-1} - F'^2_{k+1}). \quad (5.8)$$

If Equation (3.2) is used to evaluate a_k,

$$a'_k \approx \frac{(\exp(\alpha_1 A'_k + \alpha_2 A'^2_k + \alpha_3 A'^3_k))^2}{\exp(\alpha_1 A'_{k-1} + \alpha_2 A'^2_{k-1} + \alpha_3 A'^3_{k\ 1}) \cdot \exp(\alpha_1 A'_{k+1} + \alpha_2 A'^2_{k+1} + \alpha_3 A'^3_{k-1})}$$

and

$$\log_e a'_k \approx \alpha_1(2A'_k - A'_{k-1} - A'_{k+1}) + \alpha_2(2A'^2_k - A'^2_{k-1} - A'^2_{k+1}) + \alpha_3(2A'^3_k - A'^3_{k-1} - A'^3_{k+1}).$$

Following Equations (4.1) to (5.1) steps, we get an expression for $\bar{q}_k$ similar to Equation (5.1) with $\phi A'$ as

$$\phi A' = \alpha_2(2A'^2_k - A'^2_{k-1} - A'^2_{k+1}) + \alpha_3(2A'^3_k - A'^3_{k-1} - A'^3_{k+1}). \quad (5.9)$$

ESTIMATION OF CATCHABILITY

Denoting all terms of the numerators of Equations (5.1), (5.2), and (5.3) with the exception of $\log_e(C/f)'_k$ by "p" and their denominator by ϕF; the equations become

$$\bar{q}_k = \frac{-\log_e(C/f)'_k + p}{\phi f}. \quad (6.1)$$

Equating p to zero, a first estimate for $\bar{q}_k$ is obtained which is used together with catch data to estimate A', $\bar{R}_k$, $\bar{M}_k$, and $\phi A'$ so that p can be estimated and used to obtain the required estimate for $\bar{q}_k$ as well as other parameters.

If p has a negative sign, this means that the first estimate for $\bar{q}_k$ was higher than the true value and $p/\phi f$ is the correction to be subtracted to obtain the improved estimate and the reverse holds good as will be shown by the solved example. Equation (6.1) is therefore betterly transformed to

$$q_k = \frac{-\log_e(C/f)'_k}{\phi f} + \frac{p}{|\phi f|}. \quad (6.2)$$

Solved examples showed that one single correction is sufficient to obtain precise estimates for $\bar{q}_k$ for populations with increasing or decreasing abundance which is a great advantage.

If a number of equations like (6.2) are available, they may be combined in a single expression as

$$\bar{q}_k = -\frac{\Sigma \log_e(C/f)'_k}{\Sigma \phi f} + \frac{\Sigma p}{\Sigma |\phi f|}. \quad (6.3)$$

EXAMPLE

Detailed informations are required to use the equations given above for estimating correctly the catchability as dividing sampling surveys into groups coinciding with seasons having more or less constant population parameters like periods with high, low, or nil recruitment, migration, natural mortality, and catchability.

As published data reviewed by the author lacked such information, it was decided to treat the hypothetical example given by Rafail (1974) so as to demonstrate the advantage of the above modified equations. Table 2 shows a part of 1974 example containing periods I and III with increasing and decreasing abundance, respectively.

Computations for Period I

A) Surveys 1, 2, and 3

$$\log_e(C/f)'_k = \log_e(1.00118) = 0.00116$$
$$\phi f = 0.5(1{,}000\text{–}2{,}000) = -500$$
$$\bar{q}_k = -0.00116/-500 = 2.320 \times 10^{-6}.$$

Above $\bar{q}_k$-estimate is used to evaluate A', $(\bar{R}'_k - \bar{M}_k)$, and $\phi A'$ using the relations:

$$F'_k = \bar{q}_k f'_k,\ N_{k0} = \text{catch}/F'_k$$
$$\exp(A'_k) = N_{k-1}/N_k$$
$$\bar{R}'_k - \bar{M}'_k = A'_k + F'_k$$
$$A' = \bar{R}'_k - \bar{M}'^{xx}_k - F'_k.$$

TABLE 2.—A hypothetical example showing sampling periods I and III with increasing and decreasing abundance.

Period and survey k	Initial abundance N_{k0}	Effort f_k	Total mortality	Abundance coefficient A'_k	$\exp(A'_k)$	a_k	Catch $N_{k0}F_k a_k$
Period I		$\bar{q}_k = 2 \times 10^{-6}$	$\bar{M}'_k = 0.001$	$R'_k = 0.450$			
1	1,000,000	1,000	0.003	0.447	1.5636	1.26085	2,522
2	1,563,600	3,000	0.007	0.443	1.5575	1.25847	11,807
3	2,435,307	2,000	0.005	0.445	1.5605	1.25955	12,269
4	3,800,297	4,000	0.009	0.441	1.5543	1.25692	38,212
Period III		q_k 2×10^{-6}	$M'_k = 0.020$	$R'_k = 0.002$			
1	5,894,992	40,000	0.100	−0.098	0.90666	0.95245	449,175
2	5,344,753	20,000	0.060	−0.058	0.94365	0.97155	207,708
3	5,043,576	10,000	0.040	−0.038	0.96271	0.98132	98,985

where $\bar{R}'_k - \bar{M}'^{xx}_k$ is the mean of available values.

All the above relations are correct except the relation $N_{k0} = \text{catch}/F'_k$ which is an approximation of $N_{k0} = \text{catch}/F'_k \cdot a_k$. If the computations show that the calculated $(\bar{R} - \bar{M})$-values are close to each other, then the approximate expression for N_{k0} is satisfactory to obtain accurate estimates for $\bar{q}_k$. Significantly different $(R - M)$-values may also lead to accurate estimates for $\bar{q}_k$. However, it may be necessary to use $\hat{A}'_k$ to estimate a_k to obtain improved estimates for N_{k0}-values to arrive at a better estimate for A'_k and $(\bar{R} - \bar{M})$-values. The rest of the computations for period I are:

K	F'_k	$N_{k0} = C/F'$	$\exp(A'_k)$	A'_k	$\bar{R}'_k - \bar{M}'_k$	$\hat{A}'_k$
1	2.32×10^{-3}	1,087,070	1.56503	0.44789	0.45021	0.44818
2	6.96×10^{-3}	1,696,408	1.55869	0.44378	0.45072	0.44354
3	4.64×10^{-3}	2,644,181			0.4505^{xx}	0.44586

According to Equation (5.4) we get

$$\hat{A}'^2_2 = 0.1967277, \hat{A}'^2_1 = 0.2008653,$$
$$\hat{A}'^2_3 = 0.1987911$$
$$\phi A' = 0.04(0.393455 - 0.399656)$$
$$= 0.04(-0.0062) = -0.000248$$
$$\phi A'/|\phi f| = -0.000248/500 = -0.496 \times 10^{-6}$$
$$\therefore \quad \bar{q}_k = (2.320 - 0.496)10^{-6} = 1.824 \times 10^{-6}.$$

According to Equation (5.8) we can calculate $\phi A'$ by another way as

$$\phi A' = -0.08(0.4505)(13.92 - 2.32 - 4.64)(10^{-3})$$
$$+0.04(96.88 - 5.38 - 21.53)(10^{-6})$$
$$= (-0.2508 + 0.0028)(10^{-3}) = -0.248(10^{-3}).$$

That is, the two methods gave the same results.

B) Surveys 2, 3, and 4

$$\log_e(C/f)'_k = 0.0009$$
$$\phi f = -500$$
$$\bar{q}_k = -0.0009/-500 = 1.8 \times 10^{-6}.$$

The following estimates are obtained by above steps

$$\bar{R}'_k - \bar{M}'^{xx}_k = 0.44782$$
$$\hat{A}'_2 = 0.44242, \hat{A}'_3 = 0.44422,$$
$$\hat{A}'_4 = 0.44062$$
$$\therefore \quad \phi A' = 0.04(0.3946628 - 0.3898815)$$
$$= 0.000191$$
$$\therefore \quad \phi A'/|\phi f| = 0.000191/500 = 0.382 \times 10^{-6}$$
$$\therefore \quad \bar{q}_k = (1.8 + 0.382)10^{-6}$$
$$= 2.182 \times 10^{-6}.$$

The arithmetic mean for $\bar{q}_k$ from the four surveys is

$$(1.824 + 2.182)(10^{-6})/2 = 4.006 \times 10^{-6}/2$$
$$= 2.003 \times 10^{-6}.$$

Equation (6.3) can be used to estimate $\bar{q}_k$ in one step as

$$\bar{q}_k = \frac{-0.00116 + 0.00090}{-1{,}000} + \frac{-0.000248 + 0.000191}{1{,}000}$$
$$= \frac{0.002060}{1{,}000} - \frac{0.000057}{1{,}000} = \frac{0.002003}{1{,}000}$$
$$= 2.003 \times 10^{-6}.$$

Period I has four sampling surveys and only two estimates for q can be obtained as the data of only three successive surveys are used to get a single q-estimate as explained above.

Computations for Period III

$$\log_e(C/f)'_k = -0.03012$$
$$\phi f = \tfrac{1}{2}(40{,}000 - 10{,}000) = 15{,}000$$
$$q_k = \frac{-0.03012}{15{,}000} = 2.008 \times 10^{-6}.$$

The following computations are obtained according to the last estimate of catchability

K	$N_{k0} = C/F_k$	$(\bar{R}'_k - \bar{M}'_k)_1$	$\hat{A}'_1$	a_k	$N'_{k0} = C/F_k a_k$
1	5,592,318	0.00214	−0.08322	0.9595	5,828,366
2	5,172,012	−0.00788	−0.04306	0.9786	5,285,113
3	4,929,531	-0.00290^{xx}	−0.02298	0.9887	4,985,871

$(\bar{R}'_k - \bar{M}'_k)_2$	$\hat{A}'_2$
−0.01763	−0.09819
−0.01811	−0.05803
-0.01787^{xx}	−0.03795

Above estimates show a recognizable variability for the first estimated $(\bar{R}'_k - \bar{M}'_k)_1$ parameters; so the calculations are proceeded to obtain the next $(\bar{R}'_k - \bar{M}'_k)_2$-estimates which are in fact highly accurate if compared with the original values in Table 2.

Using the so-called the less accurate $\hat{A}'_1$-estimates to calculate $\phi A'$; we get

$$\phi A' = 0.04(0.0037080 - 0.0074535)$$
$$= -0.00015$$
$$\phi A'/|\phi f| = -0.00015/15{,}000 = -0.00001/1{,}000$$
$$= -0.01 \times 10^{-6}$$
$$\bar{q}_k = (2.008 - 0.010)10^{-6} = 1.998 \times 10^{-6}.$$

Using the more accurate A_2'-estimates we get

$$\phi A' = 0.04(0.00673496 - 0.01108147)$$
$$= -0.000174$$
$$\phi A'/|\phi f| = -0.000174/15{,}000 = -0.011 \times 10^{-6}$$
$$\therefore \quad \bar{q}_k = (2.008 - 0.011)10^{-6} = 1.997 \times 10^{-6}.$$

Using Equation (5.8) and the more accurate $(\bar{R}_k' - M_k')$-estimates, we get a similar result as

$$\phi A' = -0.08(-0.01787)(-0.02008)$$
$$+ 0.04(-0.0036289)$$
$$= -0.0000287 - 0.0001451 = -0.000174.$$

The above example shows that the so-called less accurate estimates gave equivalent results to the more accurate estimates. However, in situations with variable $(R_k' - M_k')$-values it will be preferable to compare their results with those to be obtained with the more accurate values.

DISCUSSION

Rafail (1974) showed the great advantages of his method for the estimation of some important parameters of fish populations like catchability, fishing mortality, natural mortality, and recruitment from catch data. He also showed that a similar analysis of data of tagged fish can allow the estimation of other important parameters like migrations and at the same time may correct the estimates of parameters of untagged fish that may be biased by unexpected recruitments and migrations.

The modifications presented here for expressions used to estimate catchability cause a great simplification, shortening of calculations and more accurate results. Rafail (1974) gave in his table 4 a summary of results of HP-20 computer programme for iteration of period I with increasing abundance. The results of the computer showed that after 16 iterations with a precision at six decimals and 22 iterations with a precision at nine decimals; q was estimated at 1.92×10^{-6} and 1.83×10^{-6}, respectively. The corresponding estimate by the present modified expressions was 1.824×10^{-6} by a single step. This simplification allowed the estimation of q from the next series of sampling surveys of period I (2, 3, and 4) so that an overall estimate of 2.003×10^{-6} becomes available which is highly accurate as the original value is 2×10^{-6}.

As far as period III with decreasing abundance is concerned, we find that 1974-expressions gave after three iterations 1.98×10^{-6} while the new expressions gave after one step 1.998×10^{-6} or 1.997×10^{-6} for q compared with an original value of 2×10^{-6}.

It is, therefore, concluded that the present modified expressions allow better accuracy and large economy in calculations and time during estimating q as compared with 1974-expressions. This greater accuracy of q will allow better estimates for other parameters. It appears what is a logic conclusion that the larger number of surveys, the larger will be the number of available q-estimates allowing a more accurate evaluation for catchability and other parameters.

SUMMARY

Modifications are presented here for expressions given by Rafail (1974) for estimating catchability to evaluate fishing and natural mortalities, recruitment, and migration assuming seasonal and subpopulation variability and the constancy of the parameters within the seasons. These modifications depend on the relation

$$(\exp(A_k') - 1)/A_k' = \exp(\pm 0.5A_k' + 0.04A_k'^2)$$

where A_k' denotes the instantaneous rate of change of fish abundance during the kth sampling period. The above expression is an extension of Paloheimo (1961) expression and gave a maximum error less than 1% when A' lies between ± 3.0 and smaller errors at smaller values of A so that the errors are less than 0.2% when A' lies between ± 2.5. This expression can be considered as highly accurate in the range that is always encountered in fisheries studies.

The modified expressions allow a large economy in calculations and time and a better accuracy for the estimation of catchability.

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IDENTIFICATION OF FISH SPECIES BY THIN-LAYER POLYACRYLAMIDE GEL ISOELECTRIC FOCUSING

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ABSTRACT

Conventional electrophoretic techniques for the identification of fish species are limited in the resolution and reproducibility needed for the reliable identification of fish species. This paper describes the potential of a high resolution protein separation technique, thin-layer polyacrylamide gel isoelectric focusing (IEF), as a new means of identifying fish species. Sarcoplasmic protein patterns are shown for 11 species of commercially important New England fishes under both low resolution (pH 3.5–10 gradient) and high resolution (pH 3.5–5 gradient) conditions. The reproducibility of the protein patterns and pH gradients from day to day is also shown. The inherent high resolution and excellent reproducibility of IEF should allow the positive identification of fish species without the costly procedure of maintaining a supply of known species for use as standards.

Many different electrophoretic techniques have been used for the identification of fish species. Protein extracts from several species of fishes were first compared using moving boundary electrophoresis (Connell 1953). Differences in the electrophoretic protein patterns between species formed a "fingerprint" for each. In an effort to obtain higher resolution and reproducibility of the protein patterns, starch gel zone electrophoresis was applied as a method for diffentiating fish species (Thomson 1960). Subsequent attempts to further improve species identification techniques centered on the investigation of new stabilizing media. The use of polyacrylamide gels (Payne 1963; Cowie 1968) and agar gels (Hill et al. 1966) resulted in shortened analysis times, increased resolution, and easier handling and storage of gels. A rapid identification technique based on cellulose acetate electrophoresis (Lane et al. 1966) has found widespread use in quality control.

Each of these electrophoretic techniques (except moving boundary electrophoresis) is still in common use and has contributed much towards eliminating problems of species substitution. Unfortunately, each of these techniques is subject to one or more limitations that lessen its effectiveness as a routine species identification test. Variations in stabilizing media composition, sample application technique, separation time, applied voltage or current, and the technician's skill indicated the need for simultaneously running known species along with unknown samples to obtain a reliable identification. Collaborative studies of the two most widely used species identification procedures, disc electrophoresis (Thomson 1967) and cellulose acetate electrophoresis (Learson 1969, 1970), showed that reproducibility of specific protein patterns from analysis to analysis was a major problem.

This paper describes the potential of a high resolution protein separation technique, thin-layer polyacrylamide gel isoelectric focusing (IEF), as a new means of identifying fish species. IEF is an equilibrium technique in which proteins are separated according to their isoelectric points in a reproducible natural pH gradient. The pH gradient is formed in the gel by the electrolysis of amphoteric buffer substances called carrier ampholytes. Protein molecules migrate in the electric field along the pH gradient until they reach the pH equal to their isoelectric point. Here the protein has a net charge of zero, and no further migration can take place. The proteins become concentrated into very sharp bands and molecules whose isoelectric points differ by 0.07 pH units (pH 3.5–10 gradient) or 0.02 pH units (pH 3.5–5 gradient) may be resolved.

PROCEDURE

Isolation of Sarcoplasmic Proteins

Fresh iced fish was obtained from various Glou-

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cester fish processors. Four specimens of each species were examined except for cod and haddock where 15 individuals each were examined. All fish were held on ice from purchase to filleting. Fillets were held at 8°C until extraction of sarcoplasmic proteins.

Sarcoplasmic protein extracts were prepared by blending 100 g of muscle tissue with 200 ml of distilled water in a 500-ml Waring[2] blender jar. A Teflon baffle shaped to fit the inside contour of the blender jar about 1 cm below the water level was used to prevent the incorporation of air bubbles during the blending operation. The distilled water, blender jar, and baffle were chilled to 8°C prior to use to prevent protein denaturation from heat generated during blending. The resulting mixture was centrifuged at 1,400 *g* for 30 min at 4°C in an International PR-2 Refrigerated Centrifuge. The resulting supernatant was used for analysis without any further purification.

Preparation of Polyacrylamide Gel Slab

The polyacrylamide gel slab was chemically polymerized between a glass plate and an acrylic template. The glass plate and acrylic template were separated by a 0.75-mm acrylic spacer that extended around three sides leaving the top open. The template had embedded teeth that formed sample wells in the gel surface. The gel slabs used in these experiments were 175 mm × 90 mm × 0.75 mm and contained 12 sample wells, each capable of holding up to 5 μl.

A 4% (wt/vol) polyacrylamide gel containing 2% (wt/vol) carrier ampholytes was prepared as follows:

Into a 25-ml Erlenmeyer flask was pipetted
- 8.2 ml distilled water
- 3.0 ml 50% (vol/vol) glycerol (final concentration 10% [vol/vol])
- 3.0 ml 20% (wt/vol) acrylamide (final concentration 4% [wt/vol]) plus 0.8% (wt/vol) bisacrylamide (final concentration 0.16% [wt/vol])
- 5.0 μl tetramethylethylenediamine (final concentration 0.03% [wt/vol])
- 0.75 ml 40% (wt/vol) ampholine of appropriate pH range (final concentration 2% [wt/vol]).

This solution was degassed under vacuum for 4 min. Polymerization was started with the addition of 50 μl 10% (wt/vol) ammonium persulfate (final concentration 0.03% [wt/vol]). After a final degassing under vacuum for one more minute, the solution was immediately pipetted into the gel mold. The top of the gel solution was layered with water to form an even surface. Polymerization was complete in 20 min at room temperature. The open top of the gel mold was then sealed with masking tape, and the whole assembly was placed in a refrigerator (8°C) overnight before use. A supply of gel slabs may be prepared and stored for 2 wk in this manner. After the gel had polymerized, the template and spacer were removed leaving the gel adhering to the glass plate.

Electrofocusing Procedure

Electrofocusing was carried out using a Medical Research Apparatus Slab Electrofocusing Apparatus, Model M-150. The gel slab was placed on the cooling platform and cooled to −2°C prior to sample application. To insure good thermal contact, a layer of light paraffin oil was used between the glass plate and the cooling platform. After the gel slab had cooled, 5 μl of the protein extract was pipetted into a sample well with a micropipette. Up to 12 samples may be compared in a single gel slab. Felt strips soaked in 1M NaOH (catholyte) and 1M H_3PO_4 (anolyte) were applied to the edges of the gel to provide electrical contact with the platinum wire electrodes. A power supply was connected to the electrodes, and power was applied until equilibrium focusing was attained. Both constant-power and constant-voltage power supplies were used in these experiments. In isoelectric focusing, a power supply capable of delivering constant power is preferred. Using a constant power of 10 W, equilibrium focusing was complete in 1.5–2.0 h. Using constant voltage, the voltage must be manually increased to compensate for increased resistance through the gel as the pH gradient forms. Separation times are longer (5–6 h) and resolution suffers due to joule heating within the gel. With either type of power supply, equilibrium focusing is attained and the reproducibility of the protein patterns is not affected. After electrofocusing is complete, the pH gradient may be measured as a check on reproducibility or to determine the isoelectric points of the separated proteins. The plate is warmed to room temperature and the pH gradient

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

is measured using a 3-mm diameter Ingold microcombination surface pH electrode and Corning Model 101 digital pH meter. The electrode was calibrated with standard pH buffer solutions at room temperature.

The protein patterns were stained with Coomassie Blue R-250 and destained in 10% ethanol–10% acetic acid (Righetti and Drysdale 1974). After destaining, the gels may be air dried and stored indefinitely.

RESULTS AND DISCUSSION

Figure 1 shows typical protein patterns for 11 species of commercially important New England fishes. The pH gradient in this gel runs from pH 3.5 at the top (anode) to pH 10.0 at the bottom (cathode). The pattern for each species appeared to be unique and demonstrated resolution not normally attained by conventional electrophoretic techniques. Closely related species such as cod and haddock or red hake and white hake show similarities in overall patterns, but enough differences are present to permit a positive identification.

Due to the large number of protein bands resolved in the pH 3.5–10.0 gradient, many of which have the same isoelectric point, it is sometimes advantageous to look at only a small portion of the pattern under increased resolution. Figure 2 shows the same 11 species compared in a pH 3.5–5.0 gradient. The resolution is much greater and identification is not complicated by the presence of as many proteins with the same isoelectric point from species to species.

Figures 3 and 4 illustrate the reproducibility of the protein patterns through a time interval. The proteins in Figure 3 were focused in 2.5 h using a constant power of 10W. The proteins in Figure 4 were focused in 5.5 h using a constant-voltage power supply. The voltage was manually increased from 100 V to 300 V in hourly 100-V intervals. The voltage was then held constant at 300 V for 3.5 h. The proteins in both plates have been focused to equilibrium, and the pattern for each species is reproducible.

The protein patterns one obtains in isoelectric focusing are dependent on the pH gradient formed in the gel. Commercially prepared carrier ampholytes form pH gradients that remain stable and reproducible during the time necessary for the complete equilibrium focusing of sarcoplasmic proteins. Figure 5 shows the pH gradients formed in the previous two figures. The pH gradient curve labeled "A" corresponds to the plate in Figure 3, and the one labeled "B" corresponds to the plate in Figure 4. The slightly lower position of pH gradient A is also seen by the displacement of the patterns in Figure 3 toward the lower end of the gel (cathode). This slight shift of the pH gradient, however, was not enough to affect the reproducibility of the protein patterns.

Isoelectric focusing offers several advantages over electrophoretic techniques for the identification of fish species. Isoelectric focusing is an equilibrium technique where the proteins are limited in how far they can travel by the pH gradient. Since proteins have a net charge of zero at their isoelectric point, no migration beyond that point can take place. Diffusion of the isoelectric proteins is prevented by the electric field. During the course of a normal electrofocusing experiment, as long as the pH gradient remains stable, the protein patterns will not vary. In contrast, protein patterns from conventional electrophoretic techniques are time dependent and may suffer loss of resolution due to diffusion.

Another advantage of isoelectric focusing over conventional electrophoretic techniques is the ease of sample application. Samples were applied directly from micropipettes into molded sample wells. Samples may also be applied as a drop or streak on the gel surface or by placing a small rectangle of filter paper saturated with the sample directly on the gel. The position of sample application may be at any point on the gel slab. While some of these sample application techniques may be common to other electrophoretic procedures, only in IEF may these techniques be used interchangeably without affecting the protein patterns. This versatility is an important asset. Dilute extracts (e.g., when the amount of muscle tissue available is unavoidably small) may be applied in a large volume to obtain a protein pattern comparable to that obtained with a small volume of a concentrated extract (e.g., a drip fluid sample from a recently frozen fish). Large sample volumes may also be applied so that minor components may be detected and compared between species. The ability to vary the position of sample application without affecting the protein pattern eliminates one more possibility for human error. Sample application technique in conventional electrophoretic methods affects the protein pattern. Samples must be carefully applied as a thin

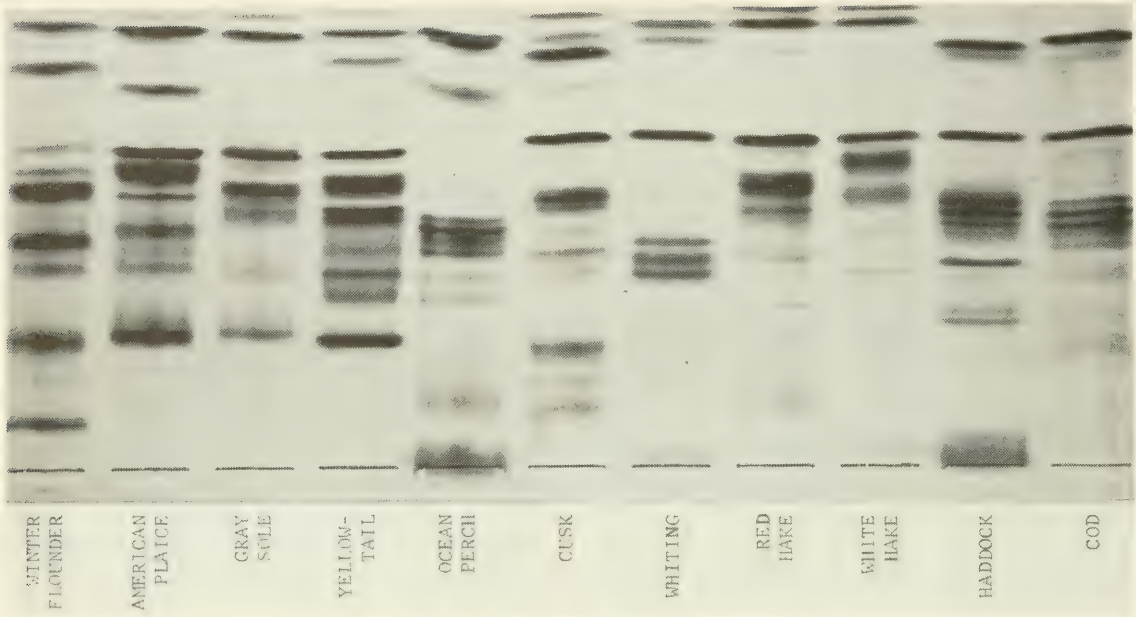

FIGURE 1.—Sarcoplasmic protein patterns from 11 species of fishes focused in a pH 3.5–10 gradient. The species are from left to right: winter flounder, *Pseudopleuronectes americanus*; American plaice, *Hippoglossoides platessoides*; gray sole, *Glyptocephalus cynoglossus*; yellowtail, *Limanda ferruginea*; ocean perch, *Sebastes marinus*; cusk, *Brosme brosme*; whiting, *Merluccius bilinearis*; red hake, *Urophycis chuss*; white hake, *Urophycis tenuis*; haddock, *Melanogrammus aeglefinus*; and cod, *Gadus morhua*.

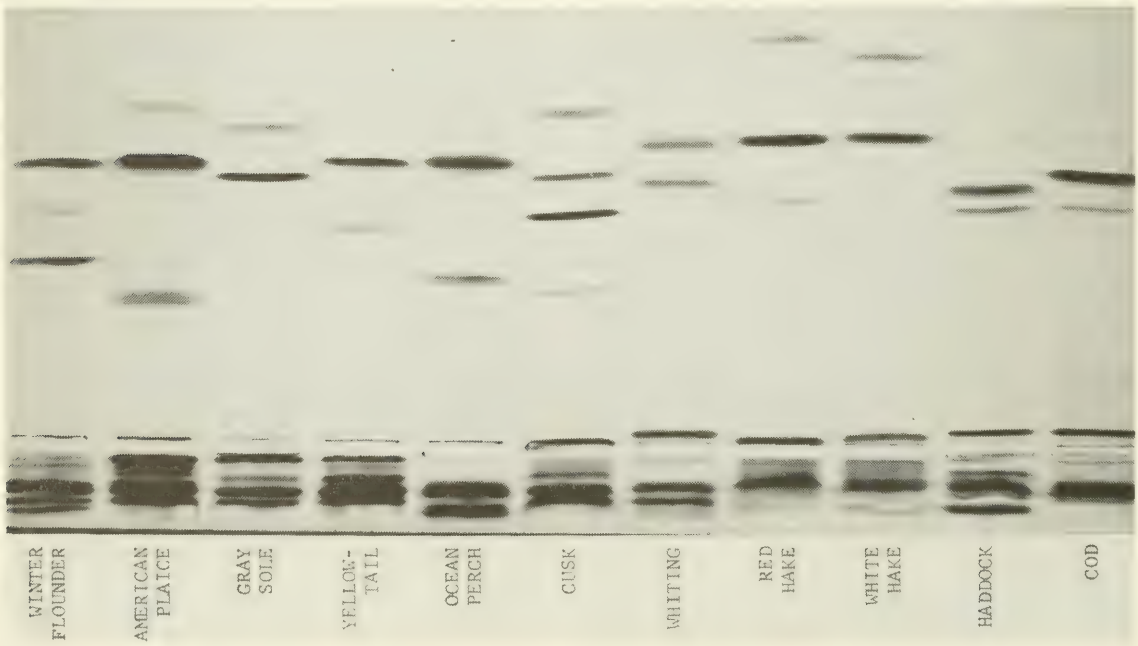

FIGURE 2. -Sarcoplasmic protein patterns from 11 species of fishes focused in a pH 3.5–5 gradient. The species arrangement is the same as shown in Figure 1. Note that the bands separated in Figure 2 correspond to the bands shown in the upper portion of the gel in Figure 1.

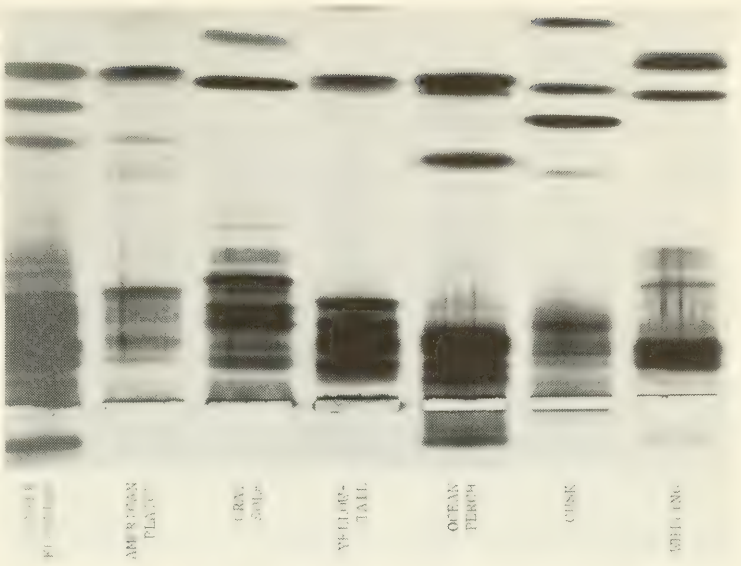

FIGURE 3.—Sarcoplasmic protein patterns from seven species of fishes focused in a pH 3.5–5 gradient under constant power conditions. The species are from left to right: winter flounder, *Pseudopleuronectes americanus*; American plaice, *Hippoglossoides platessoides*; gray sole, *Glyptocephalus cynoglossus*; yellowtail, *Limanda ferruginea*; ocean perch, *Sebastes marinus*; cusk, *Brosme brosme*; and whiting, *Merluccius bilinearis*.

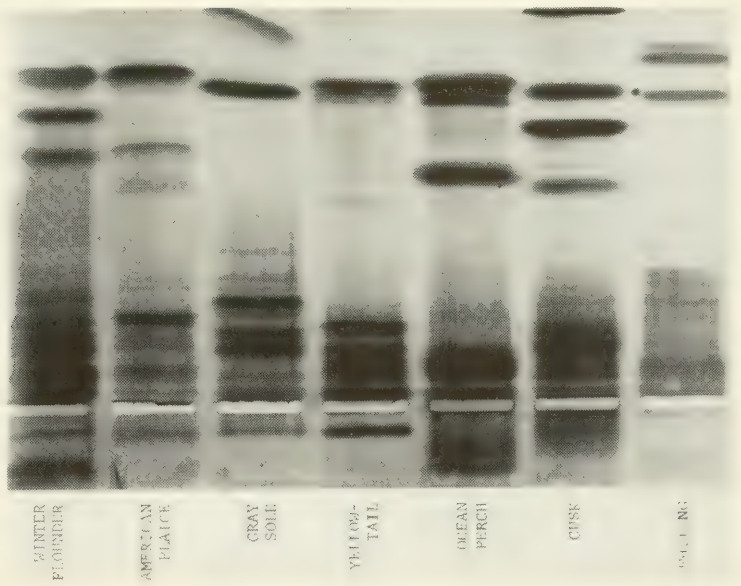

FIGURE 4.—Sacroplasmic protein patterns from seven species of fishes focused in a pH 3.5–5 gradient under constant voltage conditions. The species arrangement is the same as shown in Figure 3. Figures 3 and 4 illustrate the reproducibility of the protein patterns for seven species of fishes on two successive days.

zone at a particular position to obtain a satisfactory separation. Isoelectric focusing is actually less demanding in experimental technique when compared to electrophoresis, yet still offers increased resolution and reproducibility.

Due to the limited number of individuals and species studied, additional work is underway to increase the reliability and potential of IEF as a species identification test. Additional species will be compared. Their protein patterns will be added to a library of standard IEF protein patterns. Additional individuals from each species will be tested for variations in protein patterns due to size, sex, season, or geographical origin. Variations in some minor components of the protein patterns for some species after frozen storage have been observed. Work is planned to examine this in greater detail. The use of commercially prepared polyacrylamide gel slabs will reduce variations in stabilizing media composition and eliminate gel preparation time. These ready prepared gels used with a high-voltage constant-power

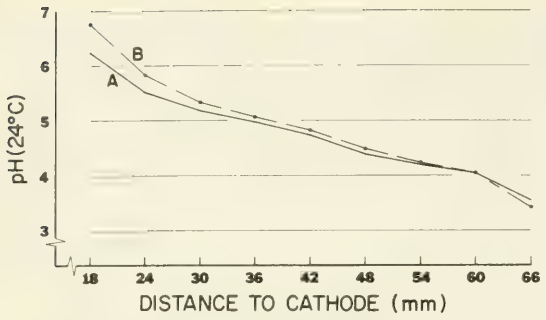

FIGURE 5.—Reproducibility of pH gradients. Measurements of pH were taken after focusing the gels shown in Figures 3 and 4. The pH gradient A corresponds to the pH measurements taken from the gel in Figure 3. The pH gradient B corresponds to the pH measurements taken from the gel in Figure 4. (The pH gradients do not match exactly because the platinum electrodes were not placed with the same relative sample well to cathode distance. The only effect this has on the protein patterns is to shift them either up or down. Relative distances between the various proteins in the pattern remain essentially the same.) The similarity of these two pH gradients may be correlated with the reproducibility of the protein banding patterns shown in Figures 3 and 4.

power supply should produce high quality sarcoplasmic protein patterns in 1.0–1.5 h. New protein staining methods have been investigated that allow staining of the protein patterns in 15–30 min with no destaining required. Using these improvements, samples may be identified in less than 2 h.

CONCLUSIONS

Thin-layer polyacrylamide gel isoelectric focusing has been shown to be a promising technique for the identification of fish species. The inherent high resolution of this method allows the production of characteristic protein patterns of a quality not normally attained by conventional electrophoretic techniques. The excellent reproducibility of this technique should allow the positive identification of fish species without maintaining a supply of known species for use as standards. Investigations utilizing commercially prepared gel slabs, high-voltage constant-power power supplies, and rapid staining techniques promise to produce an extremely reliable procedure for the routine identification of fish species.

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VARIOUS SPECIES OF PHYTOPLANKTON AS FOOD FOR LARVAL NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, AND RELATIVE NUTRITIONAL VALUE OF THE DINOFLAGELLATES *GYMNODINIUM SPLENDENS* AND *GONYAULAX POLYEDRA*

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ABSTRACT

First feeding northern anchovy larvae were presented with a variety of phytoplankters common to coastal waters of southern California to determine which species are acceptable as food. Most of the larvae ate the four species of dinoflagellates tested in feeding experiments but did not feed on diatoms or small flagellates. Larval rearing experiments were conducted to compare the nutritional value of *Gymnodinium splendens* and *Gonyaulax polyedra*, two species of dinoflagellates readily eaten by anchovy larvae and known to predominate in the chlorphyll maximum layers off the southern California coast. *Gymnodinium splendens* was a nutritional food for the first 10 days of larval life, but *Gonyaulax polyedra* was judged to be inadequate. Supplementing the *G. polyedra* diet with microzooplankton increased larval survival comparable to survival on a microzooplankton diet alone. When the *Gymnodinium splendens* diet was supplemented with microzooplankton, the larvae grew faster but survival did not increase. Results are discussed in relation to studies on larval survival in the Southern California Bight during 1974 and 1975.

The strength of a year class of fish may depend on availability of food organisms during the early larval stages (May 1974). Consequently, there have been attempts to assess the abundance of planktonic organisms in larval feeding areas as a step towards predicting year class success (Shelbourne 1957; Bainbridge and Forsyth 1971; Lasker 1975, in press). For this approach to be successful, additional information is also necessary concerning: 1) selection of prey by the fish larvae, 2) concentration and size of food organisms necessary to initiate feeding by the fish larvae, 3) nutritional value of the food that the larvae select, and 4) temporal and spatial distribution of the food organisms in the feeding area.

The northern anchovy, *Engraulis mordax*, larva has been studied in the laboratory and many criteria for successful feeding have been determined (Lasker et al. 1970; O'Connell and Raymond 1970; Hunter 1972, 1976; Hunter and Thomas 1974). Results of these studies indicate that first feeding anchovy larvae require small particles (<100 μm in smallest dimension) at relatively high densities to initiate feeding and to insure moderate survival. O'Connell and Raymond (1970) found in laboratory experiments that anchovy larvae reared in seawater containing 1 copepod nauplius/ml or less experienced heavy mortalities during the sixth and seventh days after hatching. To date such a high concentration has not been found in the nearshore region of the California Current (Beers and Stewart 1967, 1969). However, the possibility does exist that anchovy larvae could survive on some of the larger phytoplankters during early stages of development (Hunter and Thomas 1974). Lasker et al. (1970) found that anchovy larvae would feed and grow to a length of 5 to 6 mm in the laboratory on a diet of the naked dinoflagellate, *Gymnodinium splendens*. With this in mind, Lasker (1975) used laboratory-spawned anchovy larvae to test for feeding activity in seawater pumped from the surface and chlorophyll maximum layer in the nearshore region of the Southern California Bight. Lasker found that during March and April 1974 there were sufficient numbers of *G. splendens* (>20 organisms/ml) in the chlorophyll maximum layer for initiation of feeding by anchovy larvae. During 1974 and 1975, Lasker (in press) monitored the plankton distribution off the southern California coast in an effort to establish a

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relationship between oceanographic conditions and larval anchovy food organisms. In 1975 he found that *G. splendens* was replaced as the dominant organism in the chlorophyll maximum layer by the armored dinoflagellate, *Gonyaulax polyedra,* and later by a variety of small diatoms. In an effort to assess effects that this succession might have on survival of anchovy larvae, we have conducted feeding experiments with some of the phytoplankters common in the Southern California Bight to determine which species are acceptable as food by anchovy larvae. In addition, we have examined the relative nutritional value of *Gymnodinium splendens* and *Gonyaulax polyedra.*

METHODS AND MATERIALS

Phytoplankton Cultures

The phytoplankters chosen for feeding experiments are common to southern California coastal waters, and most were major components of the chlorophyll maximum layers during 1974 and 1975 (Lasker in press). Also, they were of an appropriate size for ingestion by first feeding anchovy larvae (Table 1). Axenic cultures of the selected phytoplankters were supplied by James Jordan of the Food Chain Research Group at Scripps Institution of Oceanography. Culture techniques were described by Thomas et al. (1973).

TABLE 1.—Average dimensions of phytoplankters offered as food to first feeding anchovy larvae.

BACILLARIOPHYCEAE:	
Ditylum brightwellii (25 × 150 μm, single cells)	
Chaetoceros affinis (4 μm wide in chains to 200 μm)	
Thalassiosira decipiens (8 × 10 μm, single cells)	
Leptocylindrus danicus (5 μm wide in chains to 75 μm)	
DINOPHYCEAE:	CHLOROPHYCEAE:
Gymnodinium splendens (51 μm)	*Chlamydomonas* sp. (10 μm)
Gonyaulax polyedra (40 μm)	*Dunaliella* sp. (6 μm)
Prorocentrum micans (27 × 38 μm)	
Peridinium trochoideum (20 μm)	

Feeding Experiments

To determine which phytoplankters are preyed upon by anchovy larvae, feeding experiments were conducted using methods similar to those of Lasker (1975). Cylindrical 8-liter battery jars, wrapped with dull black cardboard, were filled with approximately 5 liters of filtered seawater (filter pore size, 5 μm) and inoculated from a dense culture of the phytoplankton to be tested. The densities were determined by counting organisms in 1-ml alilquots in a Sedgwick–Rafter[3] counting chamber and/or with a Coulter Counter Model Ta, and the size was measured with an ocular micrometer. Experiments were conducted at temperatures ranging from 16.9° to 19.6°C, and the test jars were illuminated from above with a bank of four 40-W fluorescent lamps. Light intensity at the surface of the test jars was approximately 2,400 lx. Because anchovy larvae readily feed on *Gymnodinium splendens* (Lasker 1975), at least one container in each series of experiments contained only this food organism as a control to test the feeding ability of each batch of larvae.

Diatoms were maintained in suspemsion during the feeding trials by a gentle stream of bubbled air in each test jar. To evaluate the effect of such agitation on the ability of larvae to feed, experiments were conducted with and without bubbled air using *G. splendens* as food. Little effect on feeding ability could be detected (Table 2, Trial 1).

Anchovy eggs were obtained from adult anchovies maintained in spawning condition at the Southwest Fisheries Center Laboratory. Spawning techniques were described by Leong (1971). Anchovy eggs and larvae were allowed to develop in 1-liter jars (100 eggs/jar) containing filtered seawater (filter pore size, 5 μm). First feeding larvae (2.5 days after hatching at 17°C) were placed in the experimental containers with the test organism for approximately 8 h before being siphoned from the containers and quickly immobilized on a membrane filter (pore size, 8 μm) by vacuum filtration. This technique helped to prevent the larvae from defecating (Lasker 1975). The larvae remained somewhat transparent after air drying so that the presence of food in the gut could be determined by microscopic examination of the intact animal.

Larval Rearing Experiments

Anchovy larvae were reared for 10 days in 10-liter circular containers immersed in a temperature-controlled bath in an air-conditioned room (Lasker et al. 1970). The containers were filled with membrane filtered seawater (pore size, 0.45 μm), the salinity was 33.4‰, and the temperature was maintained at 16.0° ± 1.1°C. Lighting

[3]Mention of trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Laboratory feeding experiments showing the percentage of anchovy larvae that fed on: 1) diatoms—*Ditylum brightwellii*, *Chaetoceros affinis*, *Thalassiosira decipiens*, and *Leptocylindrus danicus*; 2) dinoflagellates—*Gymnodinium splendens*, *Gonyaulax polyedra*, *Prorocentrum micans*, and *Peridinium trochoideum*; and 3) flagellates—*Chlamydomonas* sp. and *Dunaliella* sp.

Feeding trial no (duration in hours)	Temp (°C)	Air-stone	Food organism	Concentration of food particles (organisms/ml)	Number of larvae per experiment	Feeding by anchovy larvae		
						% of larvae with ¼ to full gut	% of larvae with <8 particles in gut	% of larvae with empty gut
1 (7.25)	18.2		*G. splendens*	162	65	65	7	28
	18.2	X	*G. splendens*	162	54	48	9	43
	18.2	X	*G. splendens*	162	70	53	16	31
2 (8.0)	18.2		*G. splendens*	180	70	33	16	51
	18.5	X	*D. brightwellii*	164	59	0	0	100
	19.6	X	*D. brightwellii*	164	46	0	0	100
3 (8.0)	17.0		*G. splendens*	240	67	67	16	17
	17.0	X	*C. affinis*	127 chains	59	0	0	100
	17.0	X	*C. affinis*	127 chains	80	0	0	100
	17.0	X	*T. decipiens*	154	73	0	0	100
	17.0	X	*T. decipiens*	205	69	0	0	100
4 (8.0)	17.1		*G. splendens*	195	60	55	7	38
	16.9	X	*L. danicus*	197 chains	75	0	0	100
	16.9	X	*L. danicus*	780 chains	57	2	0	98
5 (8.0)	17.4		*G. splendens*	208	62	34	10	56
	17.7		*P. trochoideum*	56	65	67	22	11
	17.7		*P. trochoideum*	97	54	65	7	28
	17.7		*P. trochoideum*	210	46	50	26	24
	17.7		*Chlamydomonas* sp.	211	46	0	0	100
	17.7		*P. micans*	201	38	45	21	34
6 (8.0)	18.2		*G. splendens*	193	26	58	23	19
	18.2		*G. polyedra*	102	58	78	7	15
	18.2		*G. polyedra*	60	48	60	10	30
	17.7		*Dunaliella* sp.	303	67	0	0	100
	17.7		*Dunaliella* sp.	242	31	0	0	100

was provided for 14 h/day by 40-W fluorescent lamps as described earlier.

Eight rearing containers were inoculated with *G. splendens* and eight with *Gonyaulax polyedra* at a concentration of 100 organisms/ml. As a supplement to these food organisms, some containers were also stocked with a combination culture of the rotifer, *Brachionus plicatilis*, and the harpacticoid copepod, *Tisbe holothuriae*, with final concentrations of 0.0, 0.1, 1.0, and 5.0 organisms/ml (Table 3). Duplicate experiments were run simultaneously for all treatments including two containers without dinoflagellates but stocked with *B. plicatilis* and *T. holothuriae*, at a concentration of 5 organisms/ml.

The relative proportions of *B. plicatilis* and *T. holothuriae* (hereafter also referred to as microzooplankton) in the larval rearing containers

TABLE 3.—Survival and growth of anchovy larvae reared for 10 days on different diet regimes.

Stocking density of larvae on day 0 (no./liter)	Concentration of dinoflagellate (organisms/ml)	Concentration of microzooplankton (organisms/ml)	Survival		Standard length (mm)		Average weight (mg)
			Number	Percent	Mean	S_x	
Gymnodinium splendens							
3.3	100	5.0	11	33.3	4.24	0.359	0.039
3.4	100	5.0	15	44.1	4.87	0.671	0.048
2.2	100	1.0	5	22.7	4.30	0.480	0.061
2.5	100	1.0	12	48.0	4.73	0.677	0.047
3.1	100	0.1	13	41.9	4.46	0.355	0.046
3.9	100	0.1	6	15.4	3.57	0.314	0.046
2.8	100	0.0	9	32.1	4.23	0.485	0.042
3.6	100	0.0	8	22.2	4.03	0.413	0.056
Gonyaulax polyedra							
3.3	100	5.0	5	15.2	4.02	0.403	0.065
3.9	100	5.0	14	35.9	4.82	0.710	0.059
3.8	100	1.0	5	13.2	4.54	0.796	0.077
3.7	100	1.0	7	18.9	4.41	0.219	0.057
2.8	100	0.1	1	3.6	3.7	—	(1)
2.9	100	0.1	1	3.5	4.0	—	(1)
3.5	100	0.0	1	2.9	3.0	—	(1)
3.9	100	0.0	0	0.0	—	—	—
4.2	0	5.0	8	19.1	4.51	0.669	0.050
2.3	0	5.0	0	0.0	—	—	—

[1]Sample too small to weigh

varied during the course of the experiment. Initially, approximately 90% of the microzooplankters in the containers were *T. holothuriae*, but by the end of the rearing experiment, *B. plicatilis* was the dominant organism (97%). We were unable to determine if the anchovy larvae were selectively feeding on the copepods because the combination culture of microzooplankton which was used to stock the larval rearing containers also experienced a similar succession in species dominance during the experimental period.

Brachionus plicatilis and *T. holothuriae* were cultured together in the same vessel using techniques described by Hunter (1976). The cultures were filtered through 105-μm screening to remove the largest organisms before inoculating the larval rearing containers. Microscopic examination of the filtrate revealed a predominance of small rotifers and copepod nauplii.

Fifty anchovy eggs were added to each container the day after spawning and the appropriate dinoflagellate was also introduced at this time. Hatching occurred on the next day, which corresponds to day 0 of the experiment. The number of dead embryos on the container bottom was counted at this time and the percentage hatch was calculated. On day 2, most of the yolk sac was absorbed, the eyes were pigmented, and the larvae initiated feeding. At this time, the microzooplankton were added. The experiments were terminated on day 10; standard lengths were measured for each animal; average dry weight for larvae in each container was determined; and the percent survival in each container was calculated.

Each larval rearing container was sampled daily to monitor the concentration of food organisms. Because *Gymnodinium splendens* and *Gonyaulax polyedra* tend to form patches, 1-ml samples were taken from three different locations in the tank outside of a patch; the numbers were averaged and an appropriate amount of a dense dinoflagellate culture was added daily to maintain a concentration of 100 organisms/ml. The density of *B. plicatilis* and *T. holothuriae* was maintained in a like manner except that the volume sampled was larger (from 10- to 100-ml samples/container, depending on the stock density of microzooplankton). Also, we were careful to sample a few centimeters away from the container surfaces because *T. holothuriae* copepodids and adults are thigmotactic. We stocked the rearing containers with nauplii (which are less thigmotactic than the older stages). However, during the course of the experiments, surviving *T. holothuriae* developed beyond the naupliar stages and tended to settle out on container surfaces becoming less available to anchovy larvae. These stages were not included in our counts.

RESULTS

Feeding Experiments

A total of 518 larvae were presented with four species of diatoms (Table 2). Only one larva fed on diatoms. This single individual ate a narrow (5 × 50–75 μm) chain-forming diatom, *Leptocylindrus danicus*.

Most larvae fed on the dinoflagellates *Gymnodinium splendens, Gonyaulax polyedra, Prorocentrum micans,* and *Peridinium trochoideum*. There was no apparent preference by larvae for a particular species of dinoflagellate. Between 72 and 89% of the larvae tested fed on *P. trochoideum* (20 μm), which are as small as the smallest sized particles known to be ingested by first feeding anchovy larvae (Arthur 1976). *Peridinium trochoideum* is a darkly pigmented dinoflagellate. Perhaps this characteristic makes it more visible to the larvae than other particles of a similar size. Lasker (1975) concluded that first feeding anchovy larvae required a particle greater than 40 μm to fill their gut in 8 h.

Anchovy larvae did not feed on the smallest prey used in the feeding experiments, the flagellates *Chlamydomonas* sp. (10 μm) and *Dunaliella* sp. (6 μm).

Larval Rearing Experiments

Growth and survival of anchovy larvae reared for 10 days on different diet regimes are shown in Table 3. The survival rate of larvae reared on the *Gymnodinium splendens* diet was higher than on the *Gonyaulax polyedra* diet. The relationship between larval survival and supplementation of the dinoflagellate diet with microzooplankton was described with linear regressions (Figure 1). The survival of larvae reared in seawater containing 100 *Gymnodinium splendens*/ml did not significantly increase (t for the slope of the regression = 0.1, $P<0.20$) when microzooplankton were added to their diet as a supplement (Figure 1). Supplementation of the *Gonyaulax polyedra* diet with microzooplankton did result in a significant increase (t for the slope of the regression = 3.24,

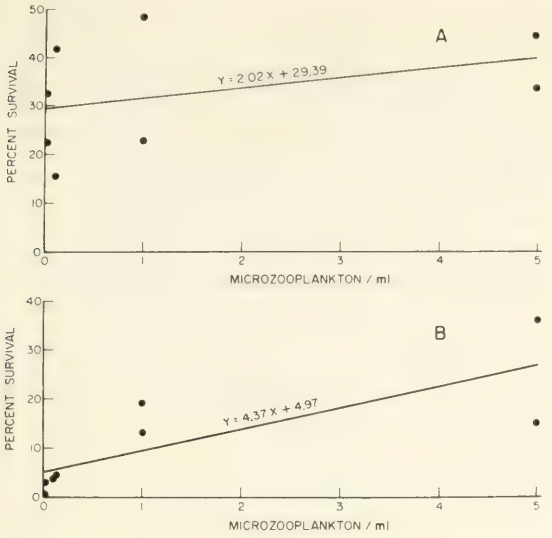

FIGURE 1.—Percent survival of *Engraulis mordax* at 10 days in relation to supplementation of a dinoflagellate diet with microzooplankton. A) *Gymnodinium splendens* diet. B) *Gonyaulax polyedra* diet.

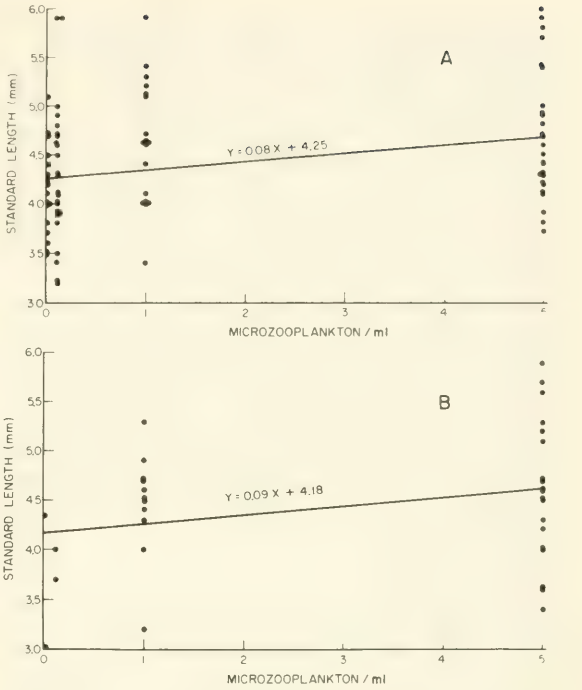

FIGURE 2.—Standard lengths of *Engraulis mordax* at 10 days in relation to supplementation of a dinoflagellate diet with microzooplankton. A) *Gymnodinium splendens* diet. B) *Gonyaulax polyedra* diet.

$P<0.025$) in larval survival. Larvae reared on a *G. polyedra* diet required at least 1 microzooplankton/ml in order to have survival rates that were comparable to larvae reared on a diet of *Gymnodinium splendens*. These results were comparable to the survival rates recorded by O'Connell and Raymond (1970) for anchovy larvae fed copepod nauplii at various concentrations. They found that larvae did not survive for 12 days in containers with less than 1 nauplius/ml.

Although anchovy larvae grow slowly during the first several days of feeding, a slight but significant increase ($t = 2.67$, $P<0.05$) in standard length occurred in larvae fed *G. splendens* when their diets were supplemented with microzooplankton (Figure 2), but no differences in dry weight were detected. Larvae fed *Gonyaulax polyedra* also appeared to increase in standard length when their diets were supplemented (Figure 2), but because the increase was slight and the number of data points was small due to the low survival rates on this diet, no significant increase was detected ($t = 1.50$, $P>0.20$).

Survival was low in larvae fed only 5 microzooplankters/ml without any dinoflagellates (Table 3). One container had no survivors and the other had 19.9% survival. Theilacker and McMaster (1971) found that larval anchovies that were fed only rotifers (*B. plicatilis*) had a lower rate of survival than those fed *Gymnodinium splendens* and *B. plicatilis* in combination. They related this finding to the low feeding success of larvae on the larger sized rotifers during the first few days of feeding. Also, Houde (1973) believes that survival of fish larvae is increased when blooms of phytoplankton are maintained in rearing containers to "condition" the water (presumably by removing metabolites).

DISCUSSION

Anchovy larvae apear to select their prey and it seems as if size is not the only criterion for selection. Larvae did not feed on any of the four species of diatoms tested in this study. The most obvious explanation is that spines and other processes on the diatoms either discouraged the larvae from striking or prevented them from swallowing. On the other hand, most larvae fed on all species of dinoflagellates tested. Visibility might also play an important role in prey selection since the darkly pigmented dinoflagellate, *P. trochoideum*,

was heavily preyed upon by anchovy larvae even though *P. trochoideum* are as small as the smallest particles detected by Arthur (1976) in the guts of larval anchovies.

It appears that prey differ in their nutritional value to anchovy larvae. *Gymnodinium splendens* and *Gonyaulax polyedra* are readily eaten by anchovy larvae, but *G. polyedra* was an inadequate food. Only 1 larva of the 74 that were reared on an exclusive diet of *G. polyedra* survived for 10 days. Larvae reared on a diet of *G. polyedra* supplemented with microzooplankton had survival rates that increased relative to the degree of supplementation. Although certain species of *Gonyaulax* are known to be toxic, it seems unlikely that this was a cause of mortality in our experiments because survival was good when larvae were fed *G. polyedra* supplemented with 5 microzooplankters/ml.

We offer two possible explanations for the difference in the nutritional value of the two dinoflagellates: 1) *G. polyedra* is about 10 μm smaller in diameter than *G. splendens*. Therefore, on the basis of volume alone, *G. splendens* could have twice as many calories as *Gonyaulax polyedra*, because the volume increases as the cube of the radius in a sphere. 2) *G. polyedra* is armored while *Gymnodinium splendens* is not, and, therefore, *G. splendens* is presumably more digestible by anchovy larvae which have an undifferentiated gut during the early stages of their development. Lasker et al. (1970) found that the armored dinoflagellate, *Prorocentrum micans* (27 $\times$ 38 μm), did not sustain life in first feeding anchovy larvae but again, this organism is smaller than *G. splendens*.

Lasker (1975) concluded that the nearshore area of the Southern California Bight was a good feeding ground for first feeding anchovy larvae during the spring of 1974 because of the high concentrations of *G. splendens* found in the chlorophyll maximum layer. In this study, the survival of anchovy larvae fed 100 *G. splendens*/ml was acceptable, and it did not differ from that of larvae fed a *G. splendens* diet supplemented with microzooplankton at concentrations up to 5 organisms/ml. Although larvae grew slightly faster when given the microzooplankton, these results still indicate that a larva could survive until an age of 10 days without the high concentrations of micronauplii that O'Connell and Raymond (1970) found to be necessary. If anchovy larvae survive to a size of 5 to 6 mm on *G. splendens*, their feeding efficiency would be higher than smaller larvae (Hunter 1972), and because of their larger size, the volume of water that larvae could search for food would also be increased. These factors would reduce the concentration of microzooplankton necessary for survival (Vlymen in press).

During several sampling periods in 1975, Lasker (in press) found that the chlorophyll maximum layer in the nearshore region of the Southern California Bight was dominated by *Gonyaulax polyedra* or a variety of small diatoms. Our work indicates that during the time periods when these phytoplankters predominated, feeding conditions for post yolk-sac anchovy larvae would be less suitable than when *G. splendens* was abundant.

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COURTSHIP AND SPAWNING BEHAVIOR OF THE TAUTOG, *TAUTOGA ONITIS* (PISCES: LABRIDAE), UNDER LABORATORY CONDITIONS[1]

BORI L. OLLA AND CAROL SAMET[2]

ABSTRACT

Courtship and spawning behavior of the tautog, *Tautoga onitis,* were observed under controlled laboratory conditions. Two separate groups of tautog, consisting of two males and one female, were each studied over an entire spawning season. The larger male of each group was dominant over the other two animals. This dominance was expressed during the spawning season by intensified aggression towards the subordinate male. The dominant male of each group, once reaching seasonal reproductive readiness, was the primary spawning partner of the female. Prior to the onset of spawning, a rapid approach of the dominant, formerly a component of an aggressive chase, functioned as a courtship behavior directed at the female. Each day the female exhibited dynamic and transient shading changes which became maximally developed as the time of each spawning approached in the afternoon. Actual gamete release, which took place each day following 6 to 8 h of courtship, occurred as the dominant male and the female moved upwards in synchrony and spawned near or at the surface. The significance of courtship and spawning in tautog is discussed and compared with reproductive behavior in other labrids.

The tautog, *Tautoga onitis,* a member of the family Labridae, occurs along the coastal regions of North America, ranging from South Carolina to Nova Scotia (Bigelow and Schroeder 1953). As with labrids in general, the fish are found associated with shelter or cover, a habit primarily related to the animals' requiring protection especially during nighttime, when they are quiescent (Olla et al. 1974).

According to previously published accounts, tautog are long-lived, reaching a maximum age of at least 34 yr (Cooper 1965) and becoming sexually mature at 3 to 4 yr of age (Chenoweth 1963; Cooper 1965; Briggs in press). The adults move offshore in the late fall to overwinter, a pattern established in field studies off Rhode Island (Cooper 1966) and off Long Island, N.Y. (Olla et al. 1974; Briggs in press). In contrast to the adults, the young remain inshore, spending the winter in a torpid condition (Olla et al. 1974).

Although a portion of the adult population remains offshore throughout the year in deep water (e.g., sports divers report finding tautog at offshore shipwrecks throughout the year), the remainder of the population moves inshore in late spring. Peak spawning activity occurs primarily in May and June (Chenoweth 1963; Cooper 1966).

From May through October adults are commonly found, especially in the midportion of their range, wherever there is appropriate cover and food supply. They are frequently seen by divers and are easily disturbed by such intrusions. The fish's reaction to divers may account for the fact that spawning in the natural environment has not been described. Spawning has also not been described under laboratory conditions. Until now the only mention of any components of a possible courtship repertoire has been by Bridges and Fahay (1968). These authors introduced a ripe male and female into a small laboratory aquarium in early June and observed transient changes in the pigmentation pattern of the female, assumed to reflect a reproductive predisposition. However, no actual gamete release was seen.

Courtship and spawning behavior in labrids has been observed in a number of species both under natural and laboratory conditions. Both paired and aggregate spawning occurs within the family. Species which have been observed to be primarily pair spawners include *Crenilabrus melops* (Potts 1974); *Halichoeres bivittatus, H. garnoti, H. maculipinna,* and *H. radiatus* (Randall and Randall 1963); *Labroides dimidiatus* (Robertson and

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Choat 1974); and *L. phthirophagus* (Youngbluth 1968). Pair spawning has also been described in *Cirrhilabrus temminckii* (Moyer and Shepard 1975), although the authors do not discount the possibility that group spawnings may occur as well in this species.

Species in which only group spawnings have been documented include *Thalassoma lucasanum* (Hobson 1965); *T. hardwicki* (Robertson and Choat 1974); and the cunner, *Tautogolabrus adspersus*, a coresident of the tautog (Wicklund 1970).

At least two labrid species have each been shown to possess both modes of gamete release. The bluehead, *Thalassoma bifasciatum*, was first seen to exhibit the dual spawning behavior under natural conditions by Randall and Randall (1963). Robertson and Choat (1974) observed similar behaviors in *T. lunare*. Both *T. bifasciatum* (Reinboth 1967) and *T. lunare* (Choat 1969) are protogynous hermaphrodites, a condition ". . . in which the individual functions first as a female, and later in life as a male" (Atz 1964). Although protogynous hermaphroditism is rather widespread in labrids (at least 30 species mentioned by Robertson and Choat 1974), until now only the two species mentioned above have been identified as possessing both modes of spawning.

Our aim in this work was to examine and describe the various components comprising courtship and spawning of the tautog. The studies were performed on adults which were held under laboratory conditions in a large aquarium.

MATERIALS AND METHODS

Two studies, spanning the 2-yr period of 1975 and 1976, were conducted on two different groups of adult tautog, with each group consisting of two males and a female. The fish were collected during late summer and early fall at Fire Island, N.Y., at temperatures ranging from 19° to 24°C. Scuba divers, using hand-held nets, were readily able to capture the fish at night when they are normally quiescent. The animals were easily identifiable with respect to their gender by the sexually dimorphic mandible, which is more pronounced in males (Cooper 1967).

The studies were conducted in a 121-kl, elliptically shaped aquarium, 10.6 × 4.5 × 3.0 m, located in a temperature-controlled room in which natural diurnal changes in light intensity were simulated (Olla et al. 1967). Layers of sand (0.6–0.8 mm) and gravel (2–5 mm), 0.6 m deep, provided a natural substrate for the fish. Beneath the gravel, seawater flowed through a network of pipes on the floor of the aquarium from a series of external filters containing sand, gravel, and oyster shells, and which provided continuous circulation and filtration. Water quality in the aquarium, operated primarily as a semiclosed system, was also maintained by addition of seawater from Sandy Hook Bay. The pH averaged 7.5, salinity averaged 24.0‰, and dissolved oxygen averaged 7.5 ppm.

It had been previously determined that in the natural environment a shelter area is a physical requirement of tautog, particularly during their nighttime quiescence. Shelter was, therefore, provided in the form of a triangular-shaped structure consisting of three clay drainage tiles (30.5 × 60.9 cm) cemented together. The shelter was placed approximately 3 m from one end of the aquarium in proximity to viewing windows. Clumps of live blue mussel, *Mytilus edulis* (5–17 kg), a major component of the tautog's diet (Olla et al. 1974), were introduced periodically to insure a continual food supply which allowed the fish to feed ad libitum. The mussels were placed 4 m from the shelter and constituted a more or less fixed feeding area.

Diurnal changes in light intensity from morning to evening civil twilight were simulated by banks of fluorescent lights mounted on the walls above the aquarium and controlled by a series of timers (Olla et al. 1967). A low level of night illumination, 0.75 lx was provided by incandescent bulbs, programmed to come on before the last row of fluorescent lights was extinguished.

Aquarium Conditions During Animals' Residency

Study 1

One male [51.5 cm TL (total length)] and one female (50.0 cm TL) were introduced into the aquarium on 20 September 1974, with a second male (59.0 cm TL) introduced 7 days later. From this point, the animals were kept in the aquarium for a total of 244 days. The fish were initially held at 19.1°C (+0.8°; −1.6°C) for 50 days. The animals were then the subjects of a long-term study dealing with the effects of temperature on activity and social behavior (Olla in prep.). Beginning at light

onset 51 days after the three fish were placed in the aquarium, the water temperature was increased during a 9-day period (mean rate 0.04°C/h) and held for 11 days at 28.7°C (+0.2°; −0.1°C). The temperature was then decreased over an 8-day period (mean rate 0.05°C/h) and held for 165 days from 14 December 1974 to 28 May 1975 at 18.7°C (+1.1°; −0.8°C).

During the first 10 days of the animals' residency, the photoperiod was decreased from 13.18 h to 12.25 h and then held constant through 22 February 1975. Beginning on 23 February 1975 the light schedule was set to conform with the natural, increasing photoperiod. The interval from 14 December 1974 to 16 January 1975 comprised the baseline nonreproductive period for Study 1. Observations on courtship behavior first began on 11 April 1975.

Study 2

Two males (54.0 cm TL and 55.3 cm TL) and one female (47.0 cm TL) were introduced into the aquarium on 28 August 1975 and kept in the aquarium for a total of 225 days. They were initially held at 21.3°C (+1.9°; −1.5°C) for 80 days. The animals were then the subjects of a long-term study dealing with the effects of temperature on activity and social behavior (Olla in prep.). Beginning at light onset of the 81st day of the animals' residency, the water temperature was gradually raised over a 9-day period (mean rate 0.04°C/h), held for 11 days at 28.7°C (+0.2°; −0.4°C), decreased during 8 days (mean rate 0.04°C/h), and then held for 115 days from 14 December 1975 to 8 April 1976 at 20.2°C (±0.7°C).

During the first 22 days of the animals' residency, the photoperiod was decreased from 14.23 h to 12.32 h and then held constant through 2 March 1976. Beginning on 3 March 1976 the light schedule was set to conform with the natural, increasing photoperiod. The interval from 14 December 1975 to 15 January 1976 comprised the baseline nonreproductive period for Study 2. Observations on courtship behavior first began on 29 January 1976.

Observation Schedule

Hourly observations made on the fish during the light period of each study consisted of 15-min readings. During each, the following measures of behavior (described in Results) for each fish were recorded for 50 counts in sequence at 18-s intervals: 1) number of aggressive interactions between fish and identity of aggressive and submissive individuals, and 2) number of courtship interactions and identity of participants. Qualitative aspects of behavior were also recorded during each reading.

During the nonreproductive period, 12 hourly observations (0700–1800 EST) were made daily in 4-day periods with intervals up to 3 days between periods. A total of 28 observation days (336 h) were made in the nonreproductive period of Study 1 and 20 days (240 h) in Study 2. During the reproductive period 8 hourly observations (0800–1500 EST) were made daily. In Study 1 these were taken in 2-day periods, with intervals up to 5 days between periods, while in Study 2 there were 4-day observation periods with intervals of up to 3 days between each. During the reproductive period a total of 15 observation days (120 h) were made in Study 1, and 13 days (104 h) in Study 2.

To compare differences in aggressive interactions prior to and during spawning, we selected 11 typical days of observations during the nonreproductive and reproductive periods of each study. Data based on the hourly means (0800–1500 EST) from these days are presented in tabular form in the Results.

Once we discovered that gamete release occurred in the afternoon on a daily basis and we had become acquainted with the reproductive repertoire of the animals, we could predict approximately when daily spawnings would occur. Therefore, in addition to the readings mentioned above, we also began to observe the fish at least 60 min and some days up to 150 min prior to and including each spawning. In Study 1 approximately 35 h and in Study 2, 25 h of observations were made prior to spawnings. During 11 typical spawning days, data collected in this fashion enabled us to determine quantitatively: 1) if there were any changes in aggression throughout the day as the spawning time approached, and 2) how close (temporally) to the spawnings, changes in courtship behavior were manifested.

Throughout each study and particularly prior to each spawning, observations were made with the use of a tape recorder. In addition, periodic motion pictures taken throughout the spawning period allowed us to analyze and interpret behavioral components and sequences both in slow motion and at stop frame.

RESULTS

Interactions Prior to Spawning Season

Prior to the onset of spawning in each study, there had developed a clear dominance hierarchy based on size, with the largest fish of each group, a male, being dominant over a smaller male and still smaller female. In turn, the smaller male was dominant over the female. Prior to the reproductive season, the majority of interactions among the three fish consisted of aggressive behavior. During various hours of the day the aggression, initiated particularly by the dominant male, served in part to limit the access of the subordinate male and female to different areas of the tank, such as the feeding area and shelter site (Olla in prep.).

Aggression was manifested at varying levels of intensity with the more intense involving the pursuit of a fleeing subordinate by a dominant, which we termed a chase. Prior to such an encounter a dominant often rapidly approached (swam towards) a subordinate. The subsequent chase could last as long as 30 to 45 s, with the fish swimming the length of the tank and at speeds reaching 100 to 150 cm/s. The most intense but rarest encounter involved a chase accompanied by the dominant biting a subordinate on any area of its body, which we termed nipping.

Aggressive encounters could also be quite subtle, with a subordinate exhibiting a change in its location, either vertically or horizontally, to a new position 0.5 to 1.0 m away, which we termed displacement. The behavior of a dominant causing this response often did not appear to differ from its forward swimming motion. Displacement of a subordinate occurred either as a dominant approached or simply turned towards it, as much as a full tank length away (10.6 m). Then there were instances in which a similar action of a dominant did not elicit any response by a subordinate. This variation in response by a subordinate was due to our not being able to assign an observable cause with regard to the actions of the dominant. We could only infer, through a subordinate's behavior, the generation of an aggressive intention signal by the dominant male.

Aggression by the dominant also caused a subordinate to assume a posture which we interpreted to be submissive, which involved the subordinate tilting its dorsal surface towards the dominant at an angle ranging from 5° to 90°. Frequently, when a subordinate was swimming about the tank and approaching an area in which the dominant was present, it would show the submissive posture as it bypassed and clearly avoided the dominant. The distance at which this would occur varied, ranging from 1.0 to 3.0 m.

Onset of Reproductive Period and Courtship Behavior

The most obvious manifestation of the approach of reproduction was the change in aggression directed toward the female by the dominant male. Beginning in early April 1975 (Study 1) and in late January 1976 (Study 2), a rapid approach of the male, which had previously represented the initiation of a chase, became functionally transformed into a component of the courtship repertoire. Now when the male approached, when within 5 to 10 cm, he veered off to one side or the other. The female was neither displaced nor showed any change in posture. We defined these acts of the male as rushes to distinguish them from approaches which formerly caused displacements and were aggressive. Rushes were directed at the female whether she was active or resting. At times as the male veered off, the magnitude of the water displacement from the force of the caudal thrusts was great enough to stir the adjacent sand and cause the female to be moved several centimeters. Rushes were observed approximately 2 wk (Study 1) and 7 wk (Study 2) prior to the first spawning.

The female, previously limited in her access to different areas of the tank, now was more mobile and concurrently began to show changes in her behavior towards the dominant. Sometimes immediately after the male's rush, the female followed him at a distance of approximately 0.5 to 1.0 m. The duration of the following behavior was usually short, lasting no more than 2 to 5 s. If the male did not initiate another rush, one of the pair simply swam away.

Another change in the female's behavior towards the dominant male was her resting in areas in which the dominant was resting. While in Study 2 this generally occurred along the walls of the tank or in the feeding area, in Study 1 it often focused around the shelter. On occasion when the dominant male was resting inside the shelter, the female often settled at the base of the structure, or sometimes actually entered and came to rest alongside the male within the same tube or in a different one.

While the female of Study 1 appeared to play a

rather passive role in stimulating the dominant male's attention (except when she simultaneously entered the shelter with him), the female of Study 2 was behaviorally much more conspicuous in attracting the attention of both males, particularly as they fed. On several occasions the female not only ingested mussels from the same small pile on which a male was feeding, but even wrested a clump of mussels from a male's mouth. This behavior was readily tolerated by both males.

In contrast to the termination of aggressive interactions between the dominant male and the female during this early prespawning period, the aggression of the dominant towards the subordinate male began to increase both in frequency and in intensity. In Study 1, aggressive acts by the dominant toward the subordinate rose from an average of 2.4/h during the nonreproductive period to 16.0/h in the week prior to the first spawning. In Study 2 aggressive acts rose from an average of 2.6/h during the nonreproductive period to 6.3/h in the week prior to spawning. Once daily spawning began in both studies, intermale aggression remained consistently high and was significantly greater during the entire reproductive period than during the nonreproductive period ($P \leq 0.05$; end count test; Tukey 1959; Table 1).

TABLE 1.—Comparison of aggressions by dominant male toward subordinate male *Tautoga onitis* for 11 days during nonreproductive and reproductive (spawning) periods of Studies 1 and 2. Data are presented as a mean of 8 h/day (0800–1500 EST) during nonreproduction and reproduction.

Study 1		Study 2	
No. aggressions per hourly observation per day ($\bar{x}$)	End count	No. aggressions per hourly observation per day ($\bar{x}$)	End count
Nonreproductive period:			
1.5	[1]–	3.0	
2.8		2.3	
3.5		3.5	
1.8		2.9	
3.3	–	2.4	
3.9		3.3	–
3.9		3.8	
0.9		1.4	
1.9	–	2.3	–
1.1	–	2.3	
2.0		1.8	
Reproductive period:			
14.2	[2]+	10.8	+
22.4	+	10.6	+
10.2	+	10.0	+
9.9	+	7.6	+
8.4	+	12.9	+
10.2	+	14.6	+
7.0	+	12.4	+
8.8	+	20.1	+
3.5		23.5	+
3.6		26.4	+
7.1	+	26.5	+
Total end count = 18		Total end count = 22	
$P \leq 0.05$		$P \leq 0.05$	

[1]– = Values for aggression during nonreproduction smaller than smallest reproduction value.
[2]+ = Values for agression during reproduction greater than greatest nonreproduction value.

The heightened intensity of aggression was reflected by the increased duration of a chase, which commonly lasted as long as 60 to 90 s with the two fish covering anywhere from 1 to 3 circuits around the tank. In both Studies 1 and 2, the other obvious factor reflecting this heightened aggression was that the dominant began nipping and biting the subordinate during chases. As a result, each subordinate male in Studies 1 and 2 bore numerous wounds on all areas of its body.

One further piece of evidence of the increased aggression of the dominant male in each study was that the subordinate male now spent the majority of time confined to either end of the aquarium, sculling in place along the wall between middepth and the surface. These locations appeared to be the ones which elicited least aggression by the dominant male.

Along with behavioral changes, external changes in the appearance of the female were also occurring with the onset of the reproductive period. Enlargement of the gonads increased the girth of the female, resulting in a more rotund appearance. At the same time, we also noted minor changes in the female's pigmentation. While prior to this period she was generally a solid dark gray, now there was a mottled white, vertical bar or stripe down the middle of each side of the body, which we termed a "saddle." At this time, the saddle was in an early stage of development (Figure 1a) of what was to be a progression of significant shading changes taking place prior to and during each daily spawning (see below for further explanation). In addition, a pale, grayish-white patch developed in the inter- and supraorbital areas of the female, giving the appearance of eyebrows. The first observations of the female's saddle were made on 11 April 1975 in Study 1 and 29 January 1976 in Study 2.

Unlike the female, the dominant male's appearance prior to and during spawning was altered very little. The only discernible shading changes of the dominant males of both studies were the development of a light gray shading covering the entire head and opercula, and the transient appearance of faint white rays (approximately 2–4 cm long) extending outwards from the orbits of the eyes. Additionally, it appeared that the ventral portion of the maxilla and the entire mandible became a lighter, almost white, shade, with the exception of the dark pores of the mandibular lateral line canals. Otherwise the male's shading re-

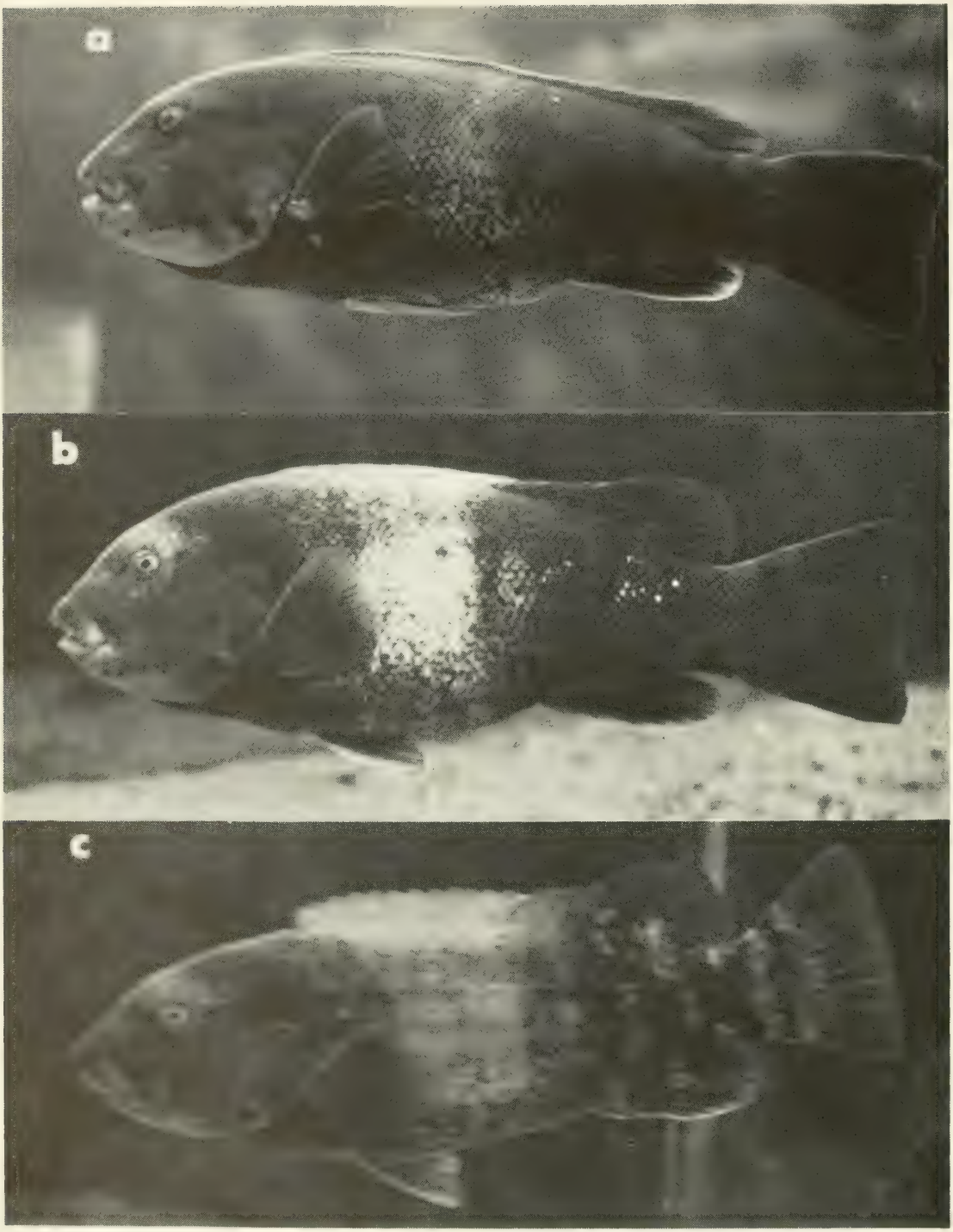

FIGURE 1.—Development of daily shading changes associated with spawning in female *Tautoga onitis*: a) earliest stage of white saddle development; b) increased size of the saddle and first, faint appearance of caudal banding as it occurs in the afternoon; c) final reproductive shading with tail-up posturing exhibited prior to spawning.

mained unchanged, with the trunk being a dark gray. Occasionally in Study 2, we noticed transient shading changes on the dominant male that were most apparent during aggression or courtship. In these cases the length of the male's midsection became a much lighter gray than the darker, dorsal area of its body. This was not a persistent change and lasted perhaps 1 or 2 min.

Development of Pair Formation

On 4 April 1975 in Study 1 (approximately 2 wk prior to the first spawning), it was apparent that there was in progress a transition from nonsexual to sexual (courtship) activities between the dominant male and female. We interpreted this to be the development of pair formation, at least within the context of the social situation and the unnatural laboratory condition.

In this same 2-wk period prior to the first spawning, the dominant's aggression directed at the subordinate male not only persisted but also began to increase and apparently served to inhibit (suppress) the subordinate's motivation to either court the female (i.e., by rushing her) and/or participate eventually in any of the spawning activities as long as the dominant was present. Since our observations in Study 1 began after courtship was under way, we were unable to ascertain the initial responses of the subordinate male toward the female, e.g., whether or not this male had originally shown any receptivity to the female (or vice versa) or attempted to court her.

In contrast to Study 1, the development of pair formation between the dominant male and female in Study 2 was slightly altered at first by the participation of the subordinate male. The dominant male had initiated rushes at the female as early as 29 January 1976 (7 wk prior to the first spawning), but then on 23 February 1976, the subordinate began to rush her periodically. In the 4-wk observation period (23 February–18 March 1976) immediately prior to the first spawning, the rushes by the dominant continued, averaging 8.8/day (range of 3–22/day), and while the rushes by the subordinate also occurred, they were lower in frequency, averaging 1.4/day (range of 0–5/day).

The events during the first and subsequent spawnings of Study 2 offered some preliminary evidence that, while gamete release was not contingent upon an established pair formation, this type of social interaction ultimately prevailed, at least under laboratory conditions. On the date of the first spawning, 19 March 1976, the female mated not with the dominant, but with the subordinate male. Although the dominant initiated some of the final courtship behavior that normally led to gamete release (see results below), and up to a point, had continued to attack the subordinate, eventually the dominant withdrew from all activities, remained inside the shelter, and did not interfere as the subordinate briefly rushed and then released gametes with the female (details described below). This type of pattern in which the dominant initiated prespawning behavior, but then withdrew and "allowed" the subordinate final access to the female for spawning persisted for 4 days through 22 March 1976.

On 23 March the dominant began taking a more active and sustained role in the final reproductive behavior. Because of this and the fact that his aggression towards the subordinate had been increasing, it appeared that the dominant might be the sole mate of the female. However, just as the dominant and female were about to spawn, the subordinate male rapidly approached the pair and simultaneously released his gametes with theirs. This pattern in which the dominant initiated and completed the spawning activities with the female, but still had not sufficiently inhibited a simultaneous spawning release by the subordinate male persisted for 7 days through 29 March 1976.

It was not until 30 March, 11 days after the first gamete release, that the spawning was completed exclusively by the dominant male and the female. Throughout the remainder of the study, the female mated exclusively with the dominant male.

Daily Reproductive Behavior

All spawnings that were observed during both Studies 1 and 2 occurred between 1330 and 1600 (EST) with the exception of one at 1015 (EST) in Study 1. The first spawning of Study 1 was on 21 April with 36 subsequent spawnings observed (1–3/day), and in Study 2 the first spawning occurred on 19 March 1976 with 22 subsequent spawnings (1–2/day).

Throughout the morning of a typical day when spawning was to occur, the dominant male was generally active, swimming about the tank, feeding, and intermittently rushing the female. Aggression towards the subordinate male usually oc-

curred right up until and after each spawning. The subordinate male continued to be restricted in its movements by the heightened aggression directed towards it and remained almost exclusively at either end of the tank, usually in midwater. The female, besides showing a minimal change in shading (i.e., early saddling, Figure 1a), as well as an occasional responsiveness to the dominant, also engaged in activities not directly related to spawning, such as feeding, swimming (with no apparent interactions with the other animals), and resting.

While the female either briefly followed after and/or rested near the dominant or exhibited no response to the rushes prior to this period, as the morning progressed she responded with progressive shading changes of varying magnitude. For example, within several seconds after a vigorous rush by the dominant male, the saddle oftentimes increased in depth and width. On some occasions the saddle took on a pale yellowish hue. The anterior half of the dorsal fin became a mottled white, ending at the same posterior border as the saddle. In addition, faint, white vertical stripes became evident on the caudal areas of the body, originating at the posterior edge of the saddle and extending just past the caudal peduncle (Figure 1b), similar to that described by Bridges and Fahay (1968). The pattern could vary, with these stripes modified into a kind of checkerboard. Along with this shading, the female often erected her dorsal fin very briefly (1–2 s) immediately following a rush.

Unless spawning was imminent, i.e., occuring within 15 to 30 min, these shading changes in the morning were retrogressive. A particular pattern might not last for more than 10 to 20 s or, at the longest, several minutes, followed by fading, with only a thin saddle persisting.

During the afternoon as the time of spawning approached (30–60 min prior to spawning), the dominant male became more responsive to the female, as evidenced by the increased intensity of the rushes. As these continued the female began to erect the dorsal fin for progressively longer periods, anywhere from 5 to 15 s. During fin erection the total area of white spanning the saddle and the dorsal fin was now maximized and, we believe, served to increase the female's conspicuousness.

In this same period she began to swim at times only with the pectorals and also intermittently began to flex the caudal fin upward. When caudal flexion first began, it usually followed a rush and was accomplished by a series of small lifts in which the female raised the caudal fin progressively higher.

The responsiveness of both the male and female was at its peak for the 15 min prior to spawning. While the number of rushes during each of the 15-min hourly observations throughout the day averaged 1.2 (Study 1) and 3.3 (Study 2), the number of rushes in this 15-min period preceding a spawning increased to an average of 6.4 (Study 1) and 9.4 (Study 2). Aggression by the dominant towards the subordinate male was not significantly different between morning and afternoon for Study 1 ($P>0.05$), but increased significantly in the afternoon of Study 2 ($P\leq0.05$; sign test; Dixon and Mood 1946; Table 2).

During the 15-min period prior to spawning, the saddle of the female was almost maximally developed, appearing whiter than it had been earlier in the day, and extending fully down the abdomen. The caudal checkerboard or striped pattern was now much more clearly defined. In addition the vent began to dilate.

The behavior of the female also began to change. She was now more active, and often swam by using only the pectoral fins. When the male moved rapidly towards her in a rush, she often erected the dorsal fin and flexed the caudal fin before the male had reached her rather than afterwards. The duration of the upward caudal flexion continued to increase. Accompanying the caudal flexion was the forward tilting of the body at about a 20° to 30° angle, serving to expose maximally the dilated vent.

TABLE 2.—Sign test comparing mean number of agressions per hourly observation by dominant male towards the subordinate male *Tautoga onitis* during the morning (0800–1100 EST) and the afternoon (1200–1500 EST) on 11 spawning days of Studies 1 and 2.

Study 1				Study 2			
Date 1975	0800–1100	1200–1500	Sign test	Date 1976	0800–1100	1200–1500	Sign test
4/28	17.0	11.5		3/24	10.2	11.2	+
4/29	24.2	20.5	-	3/25	8.0	13.2	+
4/30	4.5	16.0	+	3/29	5.8	14.2	+
5/1	8.8	11.0	+	3/30	6.8	8.5	+
5/2	7.5	9.2	+	3/31	9.2	16.5	+
5/5	7.2	13.2	+	4/1	12.5	16.8	+
5/6	8.2	5.8		4/2	8.2	16.5	+
5/12	9.8	7.8		4/5	14.5	25.8	+
5/13	4.0	3.0	-	4/6	15.5	31.5	+
5/19	2.5	4.8	+	4/7	21.2	31.5	+
5/20	3.8	10.5	+	4/8	16.0	37.0	+
No. of +			6				11
No. of			5				0
Difference			1				11
P			0.05				≤0.05

Beginning anywhere from 2 to 5 min before spawning, the female began swimming back and forth along the length of the tank close to the sand using only the pectoral fins, a behavior we defined as a run. A run was usually accompanied by a full and constant erection of the dorsal fin and the final shading development in which all of the white areas of her body (i.e., the saddle, caudal stripes or white portions of the checkerboard pattern, the "eyebrows," and the anterior half of the dorsal fin) were almost totally blanched, sometimes colored with a yellowish hue. Then, as a run was either beginning or in progress, the caudal fin was rigidly flexed upward one final time (Figure 1c), exposing the maximally dilated vent, while at the same time the head was tilted downward. The female's swimming in this position seemed awkward, resulting in her moving with a characteristic wobble or wiggle. The female made one or two runs alone which apparently served to heighten the attention of the dominant male, for he would break off other activities (e.g., chasing the subordinate male, swimming randomly about the tank) to usually rush her first and then to follow her (Figure 2a).

As the female continued on the runs, the male tended to swim more in a parallel alignment with her. Eventually he swam just slightly behind with his head moving closer to the female's operculum or midsection, 30 to 40 cm away from her (Figure 2b). Then suddenly, while increasing her speed by changing from pectoral swimming to caudal thrusts, the female swam rapidly toward the surface, with the male immediately accelerating in a similar manner to keep apace with her (Figure 2c). The angle of their ascent was anywhere from 40° to 70°. When the fish were less than a meter from the surface and while still swimming rapidly, they turned their bodies so that their ventral areas faced toward each other. On those occasions when the fish's movements were perfectly coordinated, the pectorals of the male appeared to be embracing the female (Figure 2d). With the animals in contact, they arched their bodies into U-shapes and released gametes either before reaching the surface or as they broke the surface (Figure 2e). Then the pair separated and swam downwards (Figure 2f), with the female coming to rest on the sand where the male usually rushed her 2 or 3 times within 5 to 10 s following the spawning. After a spawning, the female's shading usually regressed to just a thin saddle within a few minutes.

The spawning as we have described it appeared to comprise the prevalent mode of gamete release. However, there occurred slight variations in the

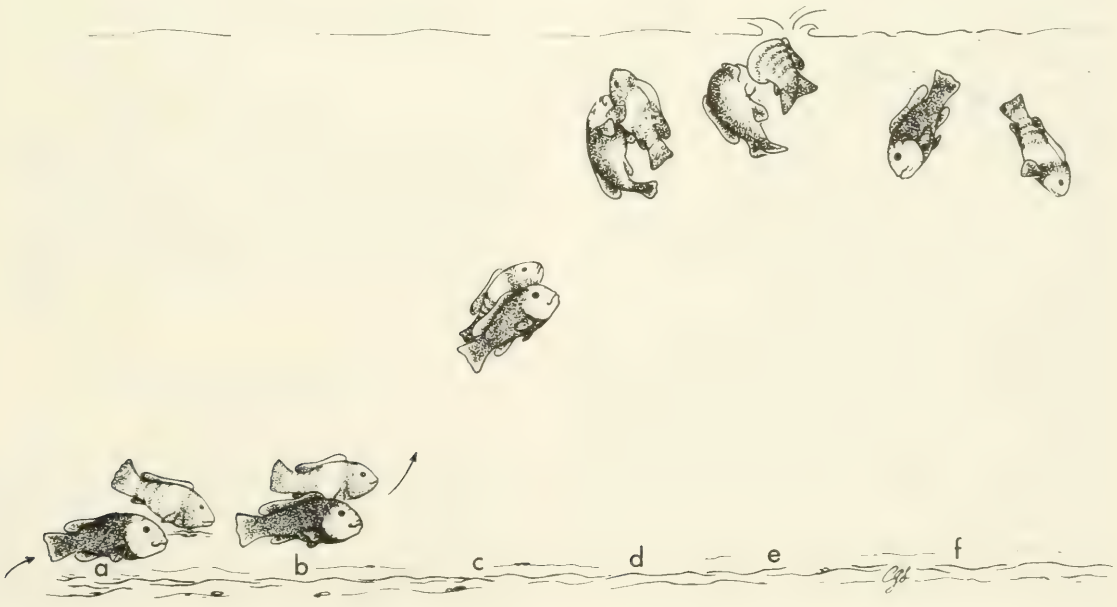

FIGURE 2.—Final sequence of behaviors leading to spawning in *Tautoga onitis*: a) male approaches female; b) they swim parallel with female slightly ahead; c) male and female move upwards in the water column; d) the pair orient to each other in a ventral-to-ventral alignment; e) with bodies flexed the pair release gametes as they break the water surface; f) the fish separate and move downwards.

behavior which still resulted in gamete release. For example, as the female was moving to the surface, rather than orienting the ventral area of her body toward the male, she bent her body into the U-shape with the result that her dorsal side faced the ventral side of the male. Gamete release still occurred as the fish flexed their bodies into U-shapes. The origin of this variation was usually due to the fact that while moving upward the female was swimming too rapidly to assume the proper alignment for the ventral-to-ventral release with the male.

A critical factor for maximizing fertilization was the breaking of the water surface at the time of release. As the fish moved upwards, churned the water, and swam downwards again, currents were created which mixed the "cloud" of gametes together. From visual observations and motion picture analysis, this occurred whether there was ventral-to-ventral or ventral-to-dorsal alignment of the pair. We would assume, however, that the most efficient method for fertilization involved the ventral-to-ventral alignment.

While runs were always performed prior to spawning, on some days there were as few as 2 runs prior to a spawning, while on other days there were as many as 11. Similarly, the duration of a series of runs varied from 30 to 180 s.

Runs were not always performed in succession. Particularly in Study 1, many times after completing one run, the pair began circling around each other in midwater. In some cases they followed each other, head to tail, along the perimeter of an imaginary circle. In other cases, as the male swam around the female, she either remained sculling in a fixed position or pivoted about her vertical axis, obviously orienting to the moving male. The total number of separate circling bouts during a run sequence ranged from 2 to 10 with a duration of each ranging from 2 to 40 s.

Occasionally at the end of a run, the pair began to swim upwards, as if to spawn. Typically, at the onset of this, the female began the transition from pectoral swimming to caudal thrusts. Moving rapidly upwards with the male alongside, the female broke away from him short of the surface and swam downwards to the sand without releasing gametes. This behavior sometimes did not occur at all while in other cases it occurred as many as six times prior to a spawning.

The continuity or fluidity of the run sequences appeared to be a critical factor serving to synchronize the fish for final release of gametes. Lack of mutual stimulatory behaviors or even slightly inappropriate behavior by one of the mates during a run, in general, were sufficient causes for a temporary breakoff of the entire sequence. During a breakoff the female's shading often regressed somewhat and she came to rest on the sand or even returned to the shelter for a few seconds.

One of the specific causes for these breakoffs was due to the fact that the dominant male, instead of maintaining his attention toward the female, chased or displaced the subordinate male which had either (actively) moved too close to the pair or (passively) happened to be in areas where the prespawning behavior was being carried out.

Other reasons for the breakoffs were inappropriate stimuli initiated usually by the male during the run sequence. In Study 1, if the male contacted the female during a run along the sand or as she ascended to spawn rather than at the apex of the pathway, the female often turned away from the male. Conversely, premature contact behavior by the male in Study 2 was an appropriate stimulus to his mate and in fact was frequently exhibited during the run sequence as well as during spawning.

Other cases in which the female initiated a breakoff from a run occurred if the male assumed an atypical position relative to hers. In Study 1, the female usually swam between the wall and the male and slightly ahead of him. Occasionally if the male assumed the position closest to the wall during a run (i.e., the female was now closer to the center of the tank) or if the male swam ahead of her, the female broke away. Since the male sometimes "corrected" his position relative to hers and hence the female did not break away, it appeared that each animal had become conditioned to a rather stereotyped set of behavioral patterns and positions which facilitated bringing the spawning to completion.

Reproductive Behavior of the Subordinate Male

In both studies each subordinate male had achieved gonadal maturation and was able to complete spawning with the female under a limited set of conditions. In each case, the reproductive behavior occurred only when the subordinate was not behaviorally inhibited by the dominant male. In Study 1, the first spawning by the subordinate male and the female occurred later in the spawning season, on the very day (29 May 1975)

that the dominant male was dying (unknown causes). This latter animal was obviously in a weakened condition and did not participate or interfere with the reproductive activities during his last day of survival. In Study 2, as described above, the subordinate male initiated courtship and spawning with the female at the onset of the reproductive season and continued until the aggression by the dominant literally suppressed all of his normal behavior.

The behavior exhibited by each subordinate male immediately prior to and during spawning was essentially comparable to that of the dominant, except that it was less stereotyped. Sometimes during a run the subordinate male weaved from one side of the female to the other; and in other cases he actually swam ahead of her on the first and second runs. Gradually as the male came to align himself more with her position, the male initiated flank contact, and positioned his body slightly above hers.

In both studies, once this continuous contact by the subordinate male was maintained, the runs, as discrete behavioral patterns, were no longer discernible. Generally the pair swam in a meandering, zig-zag pattern in midwater, and eventually circled approximately 0.5 to 1.0 m below the surface. During this behavior, it always appeared that the male was herding the female. Generally, because the pair was now so close to the surface, the final movement upwards covered only a short distance.

The subordinate male of Study 1 was last observed to spawn with the female on 25 July 1975, comprising an estimated total of 57 spawning days for this pair. Conversely, the subordinate male of Study 2 completed only 4 days of exclusive paired spawning with the female before the dominant male took an active role in the reproductive activities.

DISCUSSION

It is well known that light and temperature play a role via the neuroendocrine system in both initiating and synchronizing reproduction in fish (see review and discussion by de Vlaming 1974). However, spawning occurred in the laboratory even though the fish previously had been exposed to an unnatural photoperiod and temperature. Temperatures were, in fact, at high, stressful levels. It is possible that the endocrinological events associated with gonadal recrudescence may have been initiated 8 to 10 mo or more before the fish were captured. The photoperiod in the laboratory was eventually lengthened and regulated to keep apace of the natural changes beginning 16 days (Study 2) to 56 days (Study 1) before the first spawning. Temperatures of 18° to 20°C, well within levels at which eggs have been found in nature (Perlmutter 1939; Williams 1967), were maintained 93 days (Study 2) to 126 days (Study 1) prior to the onset of spawning.

Previously published field observations indicate that tautog spawn sometime between May and June in the waters of New York (Olla et al. 1974; Briggs in press) and Rhode Island (Chenoweth 1963; Cooper 1966), with June being the principal spawning month in Massachusetts waters (Kuntz and Radcliffe 1917; Bigelow and Schroeder 1953). These spawning dates are supported by data based on collections of eggs and larvae from Sandy Hook Bay estuary (Croker 1965) and are further extended through mid-August based on similar collections from Long Island Sound (Wheatland 1956; Richards 1959).

That the fish spawned earlier in the laboratory than they would have in nature supports the supposition that the final synchrony may depend on proximal environmental cues. While the gonadal recrudescence may have been initiated by events occurring in nature prior to capture, final synchronization may have been caused by the changes in temperature and the advancing photoperiod. Because the study was not designed to examine such questions, assignable causes of the spawning occurrence must be conjectural. Nevertheless, whatever the causative environmental events, the animals did achieve reproductive synchrony.

To date there are no specific descriptions of spawning behavior in the tautog. In a laboratory study on tautog in June 1967, Bridges and Fahay (1968) reported that during a 10-day period, a ripe female and male both underwent a shading change between 1500 and 1630 and exhibited behavior which the authors described as possible courtship. Our observations concur with these authors with respect to the daily afternoon shading alteration of the female. However, their descriptions of the behavior suggested aggressive interactions between the two animals and thus the male's shading more likely reflected an animal involved in aggression rather than courtship. The female and male's behavior further suggest that

either the animals were not in complete reproductive synchrony or the confines of the aquarium may have produced behavioral artifacts.

In our studies, pair spawning, with the dominant male tautog being the exclusive partner of the female, was the prevalent mode of reproductive activity. However, in Study 2 when spawning began, the female spawned first with the subordinate male, then both males, and finally only with the dominant. This transition period, we surmise, may have been caused by either or both of the following: 1) due to the small difference in size (1.3 cm) between the males, dominance may not have been sufficiently defined initially to inhibit the subordinate, and 2) the final phase of seasonal reproductive readiness of the dominant was slightly behind that of the subordinate. Once the dominant reached an appropriate level of sexual maturation, pair spawning involving only the dominant male and the female occurred exclusively for the remainder of the study.

Pair spawning again proved to be the mode of gamete release in our laboratory facility when a single male was in the presence of two gravid females (Olla and Samet unpubl. data). In July 1976 these two females (approximately 48 and 58 cm) were introduced into the aquarium where the dominant male from Study 2 was still residing. During intermittent observations of the fish, pair spawning occurred five times with the smaller female, although both females were rushed and exhibited a high degree of attention towards the male.

While we have never seen tautog spawning under natural conditions, it is reasonable to assume from our observations that pair spawning may play a leading role in the reproductive repertoire of this species. However, we reserve judgment as to whether this is the only pattern of gamete release, especially because of the occurrence in Labridae of both paired and aggregate spawnings within a single species, e.g., *Thalassoma bifasciatum* (Randall and Randall 1963) and *T. lunare* (Robertson and Choat 1974), both of which are protogynous hermaphrodites (Reinboth 1967 and Choat 1969, respectively).

Another factor contributing to our reserve in assigning only one pattern of reproduction to tautog is that during recent preliminary field studies, Olla and Bejda (in prep.) found sexually mature young tautog, both males and females, which were of a much smaller size and younger age than has previously been reported (Chenoweth 1963; Cooper 1966; Briggs in press). In addition, these young fish did not show sexual dimorphism of the mandible (Cooper 1967), a characteristic trait which was conspicuous in the subjects used in our studies. One explanation for the absence of the mandibular dimorphism in these young fish might be that this trait occurs in older, larger fish. Although we do now know yet whether the young animals participate in spawning, the other possibility is that these fish may represent a different sexual stage than that of the older fish of our study. It is even possible, as remote as it seems, that hermaphroditism may be present. The question is raised here because we know nothing of the behavior or gonadal development of these young fish and because hermaphroditism, in the form of protogeny, has been found in a number of labrids (e.g., 30 species according to Robertson and Choat 1974).

While it appeared that pair formation did take place within the laboratory, whether or not a true pair bonding between mates occurs in nature is still unanswered. It is possible that in their natural environment, other male tautog in the vicinity of a pair could conceivably participate at the moment of spawning. However, in these circumstances it is also quite possible that the extreme aggression of a dominant, courting male would cause other subordinate males to remain sexually passive or to move away and seek a female partner elsewhere. The hypothesis that within a given locale a dominance hierarchy among males determines which male becomes sexually active is supported by a field experiment on *Thalassoma bifasciatum* by Reinboth (1973). Additionally, it is quite possible in a natural environment that a female might spawn each day with a different male.

On the other hand, if true pair formation solely between one male and a female is possible, the selective advantage here is obvious, inasmuch as 1) it would not be necessary for an animal to expend energy finding a mate each day, and 2) to sustain its dominance (and pairing with a female) the male must continue to be a highly successful competitor. When the motivation to spawn wanes, males capable of becoming sufficiently dominant over others would have priority to act as mates.

Of all the sensory stimuli that could potentially come into play during tautog courtship, visual cues arising from the female appeared to be the most conspicuous. First, the swollen, gravid abdomen of the female, which as Youngbluth (1968)

studying the cleaning wrasse, *Labroides phthirophagus,* and Potts (1974) studying the corkwing wrasse, *Crenilabrus melops,* suggested, may have served as one of the first important visual cues to the male. In addition, the development of the female tautog's saddle, even in its most rudimentary state 2 to 7 wk before the first spawning of each study could have played an important role in identifying the reproductive state of the female. More specifically, the daily transient changes in the saddling would have served to identify the readiness of the female to spawn right up to the moment of spawning.

The existence and development of reproductive shading patterns in the female tautog is in distinct contrast with the situation found in other labrids in which the conspicuous or bright appearance, when present, is usually found in males (see Roede 1972, for review and discussion). Substantiation of the female tautog's spawning pattern was made during an observation with scuba at approximately 1500 (EST) on 26 May 1976 near the Fire Island Coast Guard Station. An adult, gravid female (approximately 45–50 cm) with a well-developed saddle was observed swimming in midwater along with a dark gray male (A. D. Martin pers. commun.). (Turbidity and the fact that the pair moved away from the diver prevented any further observations.)

Another major difference between tautog and other labrids regarding coloring or shading is that the shading change of the female was a dynamic, transient process each day. This kind of shading change in tautog falls within the category of physiological color changes discussed by Roede (1972), which reflect rapid alterations in shading and which are also reversible processes. Conversely, the descriptions of color patterns in other labrids all appear to reflect morphological color changes, which develop only gradually within each individual and particularly within discrete life phases or stages.

In concert with these shading changes were actions of the female that apparently served to enhance or facilitate the male's perception of these visual stimuli. For example, the final sustained erection of the female's dorsal fin further enlarged the white area of the saddle. Lifting of the female's caudal fin, occurring when the saddle and caudal pattern were maximally developed, was manifested in the final moment before spawning. This lift, coupled with the female's swimming near the male in such a fashion as to expose the dilating vent, provided another stimulus towards which the male could orient.

Visual shading cues arising from the dominant male appeared to be minimal except perhaps for the lightening of its face and lips. These features may have provided a stimulus to the female indicating the male's motivation to court and spawn, particularly during rushes directed at the female's head. The stimulus value of the male's white lips during courtship displays in *Crenilabrus melops* has also been suggested by Potts (1974).

The obvious visual cues of the male, arising from its rapid approach during a rush, were quite likely a primary source of stimulation to the female. It is also possible that there was a secondary, lateral-line stimulation, created by the force of the water currents as the male rushed by and which may have enhanced the overall response of the female. Other potential stimuli arising from either of the mates may have been chemosensory in origin. We have no basis at this point to conjecture whether or not the animals released and/or perceived any chemical products (i.e., pheromones), which may have functioned to facilitate reproduction.

An important indicator of the approaching onset of the reproductive season was the change in behavior of the dominant male towards the female. It gradually ceased being aggressive to the female, initiated courtship rushes, and permitted her unrestricted access to any area of the tank. This behavioral transition from aggressive to courtship activities is very similar to that observed in *Crenilabrus melops* (Potts 1974). In this species, which pair spawn at a nest site, the nesting male is aggressive to both males and females at the onset of the reproductive period. Eventually, however, instead of approaching a female to chase or bite her, the male performs an exaggerated courtship, swimming around the female which apparently stimulates her to approach the male and his nest.

As with many other species, each of the courtship activities of the tautog seem to serve one major purpose, which was the gradual excitation and synchronization of the partners prior to the spawning each day. In the extended period before the very first spawning of the season, the dominant male appeared to assume the more physically active role in the early courtship, primarily by rushing the female. While the female did occasionally follow after or rest near him, she did not perform any obvious (ritualized) activities. Nevertheless, even the slight shading changes in

her saddle during a rush may have functioned as a type of response, communicating to the male her receptivity and possibly her altering physiological state.

Once the first and subsequent daily spawnings began, it appeared that the female now set the tempo for synchronizing the events leading to spawning. The first "signal" that spawning was imminent occurred when the female's caudal stripe or checkerboard pattern was consistently maintained, followed by a further broadening and blanching of her saddle. Then, once her pectoral swimming, the tail lift, and head-down behaviors were sustained, the female initiated the final courtship behavior (i.e., runs). Even though the male synchronized his movements with hers, the pace and completion of the runs and upward spawning motion were contingent on the female's actions.

The separate behavioral components of the courtship and spawning repertoire in the tautog reflect both similarities and differences when compared with other labrid groups. In the cleaning wrasse, *Labroides phthirophagus,* pair formation and courtship precede spawning by at least a week or more (Youngbluth 1968). During this time the male repeatedly performs rapid approaches ("passes") towards the side of the female which she tolerates; however, the male's action in this case is generally also accompanied by a body quivering. In some species the only vigorous approaches by males toward females are described as chases, such as in the four *Halichoeres* species observed by Randall and Randall (1963); the cunner, *Tautogolabrus adspersus* (Wicklund 1970); *Thalassoma bifasciatum* (Randall and Randall 1963); and *T. lunare* (Robertson and Choat 1974). In *Cirrhilabrus temminckii* the male performs a single rushing action similar to the tautog, but this only occurs immediately prior to the upward darting for gamete release (Moyer and Shepard 1975).

In many of the species described above, the males also perform ritualized swimming patterns or displays to attract the females. These have been described as circling, looping, fluttering, dancing, or simply courtship swimming. The responses of females among the various species can vary from a simple approach such as in *T. bifasciatum* (Reinboth 1973) to an over, reciprocal response such as "sigmoid posturing" and "dancing" as in *L. phthirophagus* (Youngbluth 1968), or a lateral approach to the male in which the swollen flank and genital papilla are presented as in *Crenilabrus melops* (Potts 1974).

With the exception of *C. melops* which spawn on the sand in a nest, all of the other species mentioned above and tautog share a common mode of swimming or darting rapidly upwards to spawn. Body bending (only by the male of a pair) in *T. bifasciatum* has been observed by Reinboth (1973) as well as the brief alignment of the pair's genital openings.

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DISTRIBUTION, SIZE, AND ABUNDANCE OF MICROCOPEPODS IN THE CALIFORNIA CURRENT SYSTEM AND THEIR POSSIBLE INFLUENCE ON SURVIVAL OF MARINE TELEOST LARVAE[1]

DAVID K. ARTHUR[2]

ABSTRACT

The California Current system can be divided into onshore and offshore faunal zones by a copepod indicator species, *Mecynocera clausii*. Near the outer edge of the onshore zone copepod nauplii densities were higher than usual. There were about 3 times as many microcopepodids and 12 times as many nauplii on the average throughout the onshore as in the offshore zone. Feeding habits of larvae of sardines, anchovies, and jack mackerel may be adapted to the usual naupliar and copepodid concentrations of the zone in which they were spawned. The usual concentration of 56-μm and wider nauplii in the onshore zone was about 3/liter with 17/liter the highest observed which indicates that for nauplii of all sizes there were usually about 36/liter and with the highest density of 195/liter. These concentrations are lower than has usually been reported to be required for rearing larval fish in laboratories. Numbers of nauplii decreased exponentially with increasing size but a naupliar biomass maximum was found to occur at about the 70 μm width. Nauplii of this size are ingested at first feeding by Pacific sardine, northern anchovy, and jack mackerel larvae. It is suggested that larval feeding habits of these fish have evolved to utilize this important food resource at their first feeding.

Copepods form the bulk of most zooplankton hauls from the sea and are important because they are the main convertors of phytoplankton into food suitable for higher organisms (Marshall 1973). Copepods are especially important as food for planktonic larvae of pelagic marine teleosts. Food of the larvae of commercially important marine fishes has been widely reported as being primarily eggs, nauplii, and copepodid stages of small copepods. Yokota et al. (1961) found that food occurring in the feeding larvae of all the 57 species taken in their primarily coastal samples was almost entirely small copepods, especially nauplii. Duka and Gordina (1973) investigated the food of larvae of 26 species of teleosts from the Mediterranean and adjacent areas of the Atlantic and reported that copepod nauplii composed 90% of all items eaten by small larvae (2.3 to 5.0 mm). Stomach content analyses of fish larvae are also corroborated by population dynamic studies of plankton organisms. Fish (1936) noted that in the Gulf of Maine a small copepod, genus *Pseudocalanus*, suffers a much higher predation rate during the naupliar stages than does *Calanus finmarchicus* whose eggs (140 μm wide) and nauplii are too large to be ingested by many fish larvae.

When it became apparent that the population of Pacific sardine, *Sardinops sagax*, was in serious decline, a research program [later to become known as CalCOFI (California Cooperative Oceanic Fisheries Investigations)] was initiated in 1949 to investigate the ecology of this important fish. One part of this investigation was a study of the food and food resources of sardine larvae and consisted of two main objectives: 1) determine what the larvae eat, and 2) to study the abundance and distribution of these food items. The ultimate purpose was to determine if feeding conditions, especially for the first feeding larvae, could be a contributing factor to the sardine's decline, as was proposed by Hjort (1914) to explain poor year class survival of fishes in general.

The identifiable food of first feeding sardine larvae was primarily copepod nauplii ranging from 25 to 80 μm but mostly about 70 μm wide (Arthur 1976). Nauplii of this size are produced only by small species of copepods, roughly less than 1.5 mm long. The assemblage of these small copepods is composed of many species. Several genera have often been recorded as being abun-

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dant in the plankton as well as in the intestinal contents of larval fishes. Among these are the cyclopoid genus *Oithona,* (especially *O. similis*), and the calanoid genera *Pseudocalanus* and *Paracalanus. Oithona similis,* whose first stage nauplius is 70 μm wide (Oberg 1906) and can, therefore, be ingested by sardine larvae, composed over 50% of the cyclopoid fauna in 37 of the 42 samples off Oregon through Baja California examined by Olson (1949). Because of the large number of species, many of whose developmental stages had not been described, no attempt was made in this study to identify eggs, nauplii, and copepodid stages to species.

This report deals with size, abundance, and distribution of naupliar and copepodid stages of copepods captured with relatively fine meshed plankton samplers in and near the California Current. These small species of copepods will be referred to as microcopepods, and all postnaupliar stages, including adults, as copepodids. The term nauplii will include true nauplii and metanauplii.

SAMPLING METHODS

The need for a study of the small crustacean plankton was anticipated early in the CalCOFI program. The 1-m net with its relatively coarse mesh (505 μm) was considered adequate for sampling sardine eggs and large copepods and euphausiids, but most small copepods and nauplii pass through this size mesh. Starting in May 1949, a Clarke–Bumpus sampler (Clarke and Bumpus 1940) equipped with a #8 mesh bolting silk net, (203 μm in unused condition) was used routinely at stations in the central and upper southern California areas. It was towed obliquely from a depth of 70 m, filtering about 5 m^3 of water.

The Clarke–Bumpus sampler was abandoned after March 1950 in favor of the "high-speed sampler" (California Academy of Sciences et al. 1950) which was modified by having a mouth diameter of 7.6 cm, the same as the main fuselage of this device, rather than being tapered to a narrower opening as in the original high-speed sampler. It was equipped with a 143-μm wire filter and was towed on the same wire as the meter net and was used because the record it made of depth versus volume of water filtered could be used to analyze the meter net track as well as its own. This modified version was called the "microplankton sampler." It was towed obliquely from a depth of 70 m during March 1950–September 1950 and from 130 m on cruises from November 1950 to July 1952.

After a study had been made of the food ingested by ocean-caught sardine larvae, it became obvious that very small copepod nauplii are critical in the ecology of these larvae. Therefore, after August 1951 a plankton sampler of much finer mesh was used. This sampler was essentially a medium Epstein net (Sverdrup et al. 1942:379) with a mouth opening 17.5 cm in diameter, connected by a canvas collar to a filtering cone constructed of #20 bolting silk (76 μm in unused condition). This sampler was hauled vertically from a depth of 50 m and was called the "truncated net."

These three plankton samplers were used between May 1949 and September 1954. Pertinent statistics are compared as follows:

	Mouth diameter	*Mesh aperture size (μm)*		
Sampler	*(cm)*	*New*	*Used*	*No. of samples*
Clarke–Bumpus	12.5	203	120	185
Microplankton	7.6	143	143	612
Truncated net	17.5	76	56	239
				1,036

Because of expansion when wet, and the unraveling of threads when used, the aperture size of used wet silk nets is considerably smaller than new dry ones. The above "used" values were obtained by measuring aperture sizes, when submerged in water in the laboratory, of nets being used in the collections. Even with the smallest aperture size used (56 μm) many nauplii and copepodids must have escaped. Beers and Stewart (1967) reported that a significant quantity of copepods pass through a 35-μm mesh. Most food particles of sardine, anchovy, and jack mackerel larvae, however, are wider than 56 μm (Arthur 1976.)

COUNTING METHOD

The plankton samples were examined in a plastic chamber measuring 60 mm by 70 mm, the floor of which was lined every 5 mm to form a grid. Its total fluid capacity is approximately 50 ml with a water depth of about 12 mm. In practice, the fluid volume in the chamber measured less than half of this. If the amount of material in the sample was not too great, the entire sample was counted. Most samples taken with the Clarke–Bumpus and truncated nets contained so much material that subsampling was necessary. This

was accomplished by first measuring the total fluid volume of the sample, then stirring it vigorously to disperse the material, then drawing off a convenient amount for examination, and finally measuring the remainder in order to determine what percentage the subsample was of the original sample.

FAUNAL AREAS IN THE CALCOFI SECTOR

Although the primary purpose of the microplankton program was a quantitative appraisal of the microcopepod fauna, a few prominent copepod species were routinely recorded. One of these, *Mecynocera clausii,* proved useful as an indicator organism allowing the CalCOFI sector to be roughly divided into two plankton faunal areas, onshore and offshore.

Mecynocera is a monotypic genus. It can readily be distinguished from other copepods by its exceptionally long first antennae (Mori 1964). Its small size (about 1 mm) places it within the microcopepod range. These attributes make it convenient and useful as an indicator of conditions affecting the microcopepod fauna. *Mecynocera clausii* has been reported near the surface throughout tropical areas of the oceans, as well as in temperate areas such as the Mediterranean. In the CalCOFI area its presence may be considered as indicating the more tropical offshore and southern waters.

A typical distribution of *M. clausii* off southern California and off northern and central Baja California is illustrated by data for February 1951 (Figure 1). *Mecynocera* is characteristic of offshore water whereas the occurrence of plutei of benthic echinoderms may indicate coastal water. The two boundaries tend to interdigitate, which must imply alternating tongues of warm offshore water penetrating toward the coast and jets of cold onshore water moving out to sea. The 15°C isotherm supports this interpretation.

Submergence of the water of the California Current under the offshore subtropical water may be indicated at stations where *Mecynocera* and plutei were taken together. This would result if the net in its 130-m deep track caught *Mecynocera* near the surface and plutei at some depth where the submerging water had carried them.

The shoreward boundary of *Mecynocera,* as determined by the various cruises, is presented in Figure 2. In general, the average boundary is

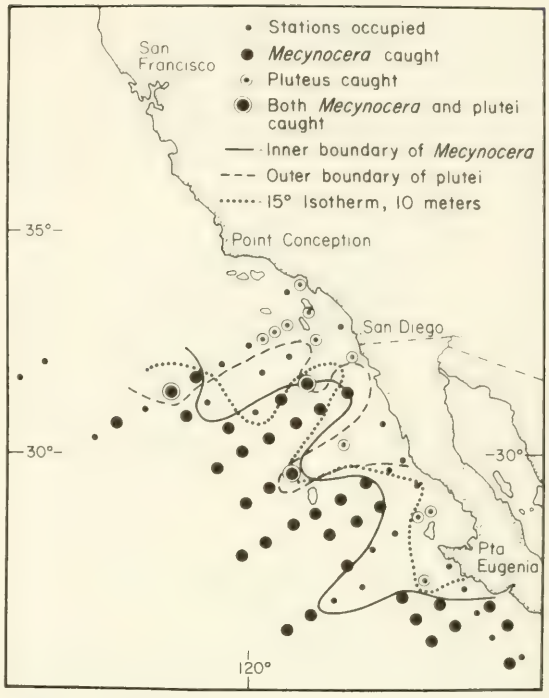

FIGURE 1.—Distribution of *Mecynocera clausii* and pluteus larvae during CalCOFI cruise for February 1951 off California and Baja California.

found about 400 km offshore in the San Francisco area and inclines toward the coast farther south. In the northern Baja California area it may impinge upon the shoreline, but it becomes erratic in the turbulent Punta Eugenia area.

ZONE OF COPEPOD NAUPLII MAXIMUM

For a given cruise, if each line is examined and the station which contained the greatest concentration of nauplii is circled and the circled stations for the various lines are connected, one obtains a line of maximum copepod nauplii concentrations. Figure 3 presents a typical distribution of copepod nauplii and their maximum zone in the Channel Island area. Two stations have been circled for the line extending offshore from San Diego. It is common to find a high local concentration at stations near the coast and a second high offshore particularly in the area north of Point Conception. Had the station pattern extended closer to the beach, higher concentrations of nauplii probably would have been encountered there. During a 5-mo

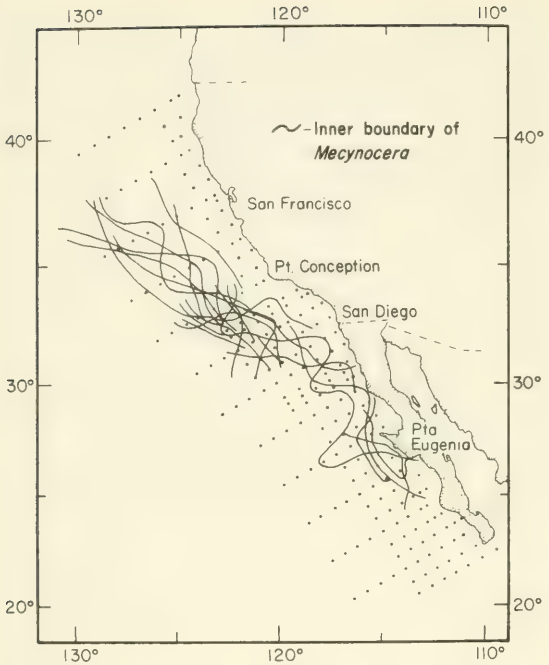

FIGURE 2.—Inner boundary of *Mecynocera* for individual CalCOFI cruises from June 1949 to July 1951 off California and Baja California.

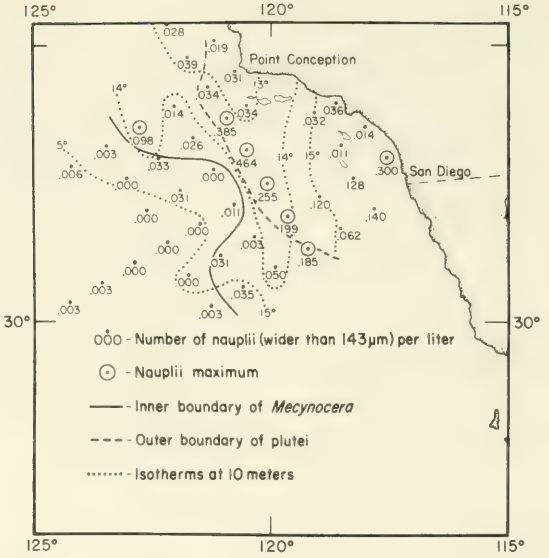

FIGURE 3.—Distribution of copepod nauplii (wider than 143 μm) and their relation to some other biological and physical variables during June 1950.

study of plankton off La Jolla, Beers and Stewart (1970), using 35-μm mesh nets, found that for the three stations located 1.4, 4.6, and 12.1 km from shore, naupliar densities averaged 63/liter, 33/liter, and 26/liter, respectively.

The zone of maximum nauplii seems to be associated with the *Mecynocera* boundary, which is also indicated in Figure 3. The station of maximum nauplii for a line usually occurs one to three stations onshore of this boundary.

As may be seen in Figure 3, there appears to be an association between the zone of maximum nauplii and the tongue of relatively cold water (13° and 14° isotherms) extending south of Point Conception. This cold tongue probably is nutrient rich water upwelled north of Point Conception. Shoreward from this zone lies the counterclockwise gyre of the Southern California Bight, extending from Point Conception to northern Baja California. Allen (1939) stated that his most offshore station, located 120 km from the coast, which is in the general vicinity of the nauplii maximum, was consistently the richest station for microcrustacea. Berner (1959) noted that stations where he found anchovy larvae to be feeding were in the area of the copepod nauplii maximum as described by Arthur (1956).

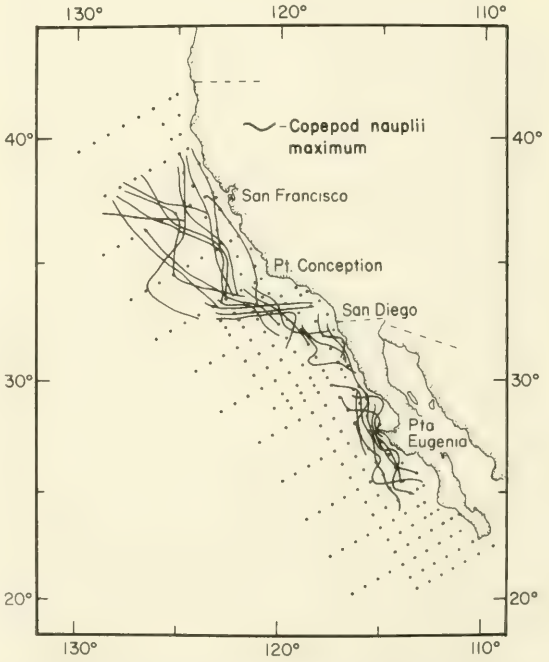

FIGURE 4.—Copepod nauplii maxima for individual CalCOFI cruises from June 1949 to July 1951.

In the San Francisco area, where two maxima are commonly found, the outer one is usually about 115 to 400 km offshore (Figure 4). The maximum zone is consistently found seaward from the Channel Islands, about 100 to 320 km off the mainland shore. Occasionally nauplii-rich stations are found inside the islands. The average nauplii maximum approaches the coast south of San Diego, and is adjacent to the shoreline in northern Baja California, probably a result of upwelling along the coast. From Punta Eugenia south, this zone becomes irregular, as does the *Mecynocera* boundary.

QUANTITATIVE DISTRIBUTION OF MICROCOPEPODIDS AND NAUPLII IN THE CALCOFI AREA

On examining the values obtained in this program, it is apparent that there are very wide ranges in densities. Values for microcopepodids range from 0.003 to 7.886/liter. Nauplii were sampled in numbers ranging from 0 to 17.280/liter. Frequency distributions are highly skewed toward the lower densities. To overcome this problem, the data are presented as logarithms to normalize the frequency distributions.

The method used for comparing data is the ogive, or cumulative frequency curve. The ogive is useful to depict what percentage of the samples from an area contains any particular concentration of copepodids or their nauplii. Furthermore, in considering concentrations of any two areas, the value of the 50 percentile concentrations can be quickly read off and compared. The 50 percentile value in this particular type of distribution lies very near the mode and so may be considered to closely represent the most common value of concentration for a given area.

Ogives for nauplii and microcopepodids as sampled by all Clarke–Bumpus and all microplankton samples in both the onshore zone and offshore zone are presented in Figure 5. Because of the large mesh size of the nets used, most nauplii escaped which resulted in more copepodids than nauplii being caught. The truncated net (56-μm mesh) caught more nauplii than copepodids. Very few samples were taken in the offshore zone with the truncated net and so it cannot be compared with the other two samplers in this manner. Differences in the ratios of onshore zone to offshore zone for the 50 percentile values are as follows:

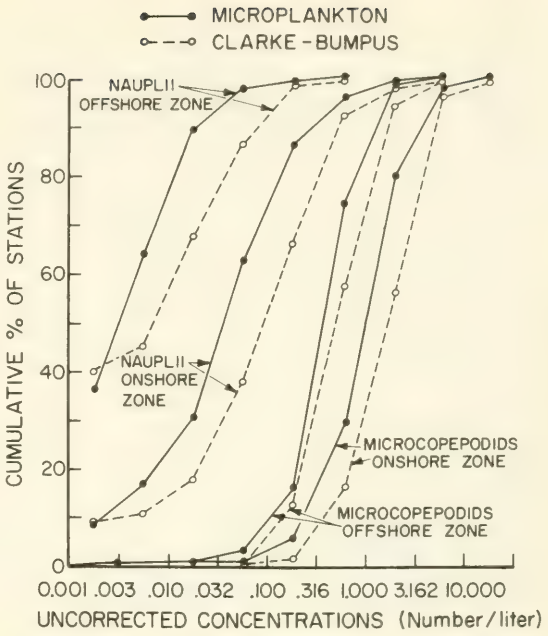

FIGURE 5.—Ogives for abundance of nauplii and microcopepodids in offshore and onshore zones as sampled with the Clarke–Bumpus (120-μm mesh) and microplankton samplers (143-μm mesh).

Sampler	*Microcopepodids*	*Nauplii*
Clarke–Bumpus	3.17:1	12.58:1
Microplankton	2.57:1	11.22:1

There are about two and one-half to three times as many copepodids in the onshore zone as there are in the offshore zone. There are, however, about 12 times as many nauplii in the former as in the latter. There are about four times as many nauplii per copepodid in the onshore zone as in the offshore zone. This is probably a result of the increased fecundity of copepods living in the richer phytoplankton owing to upwelling in the onshore zone.

CORRECTING FOR CALIBRATION ERRORS AND ESCAPEMENT

The ogive was useful to correct errors of the various samplers used in this survey. Figure 6 presents the ogives obtained for microcopepodids by all samples taken in the onshore zone with the three different samplers. Of the three samplers, the Clarke–Bumpus was the most accurately calibrated for volume and so the other two samplers were corrected to it. Such a correction can be made

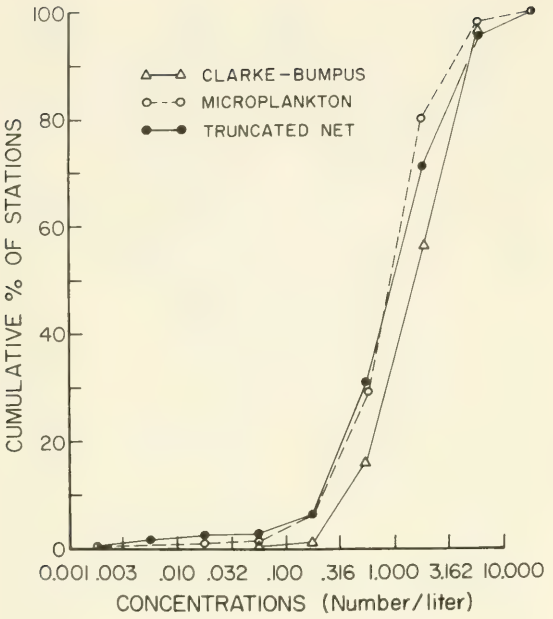

FIGURE 6.—Ogives for abundance of microcopepodids in the onshore zone as sampled by the three samplers.

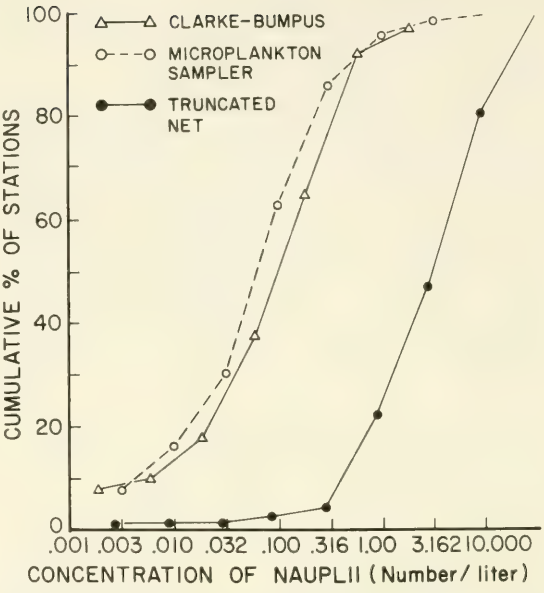

FIGURE 7.—Ogives for nauplii of all sizes retained by each of the three samplers in the onshore zone corrected for volume filtered.

by measuring their 50 percentile differences and adding this value to all the points along their respective curves. This correction assumes that all net meshes used retained copepodids in equal percentages. This is not entirely correct as Beers and Stewart (1967) reported that some copepodids can escape even a 35-μm mesh.

Having corrected the volume errors of the three devices (or, at least, made them comparable in value), we can now roughly correct for the amount of escapement by nauplii through the three different mesh sizes. Figure 7 presents ogives for nauplii in the onshore zone as sampled by the three devices, the numbers of which have been corrected for volume strained by values obtained by the 50 percentile differences in Figure 6. These ogives are based upon the same amount of water filtered, thus their differences are due to differential escapement of nauplii. By comparing the 50 percentile values in Figure 7, the following approximation of the size distribution of the naupliar population in the onshore zone is obtained:

Sampler	*Mesh opening (μm)*	*Usual number retained/liter*
Truncated net	56	2.884
Clarke–Bumpus	120	0.095
Microplankton	143	0.058

A plankton net hauled from some depth to the surface may pass through a wide range of plankton concentrations but its catch will represent only the average of these conditions and will not reveal rich but thin strata that might exist. The above concentrations, therefore, probably underestimate somewhat the highest concentrations found in the usual water column.

When the ogives for the three samplers are corrected to the Clarke–Bumpus for volume and to the truncated net for escapement, by their 50 percentile differences (Figure 8), they are similar over the mid-60% of their ranges. It is interesting that the three curves for nauplii are so similar when it is considered that two of them represent, primarily, the small percentage contributed by larger nauplii. This implies that the various sizes of nauplii have essentially the same type of distribution and with the same degree of patchiness.

The slope of an ogive is determined by the degree of dispersion within the samples. If the distribution of an organism is so homogeneous that all the observations should fall in one interval, then the resultant ogive would be a vertical line. With wider ranges of densities the ogive will slope less abruptly. By comparing slopes of the two sets of ogives in Figure 8, it can be seen that the copepodid stages are more uniformly distributed than are nauplii.

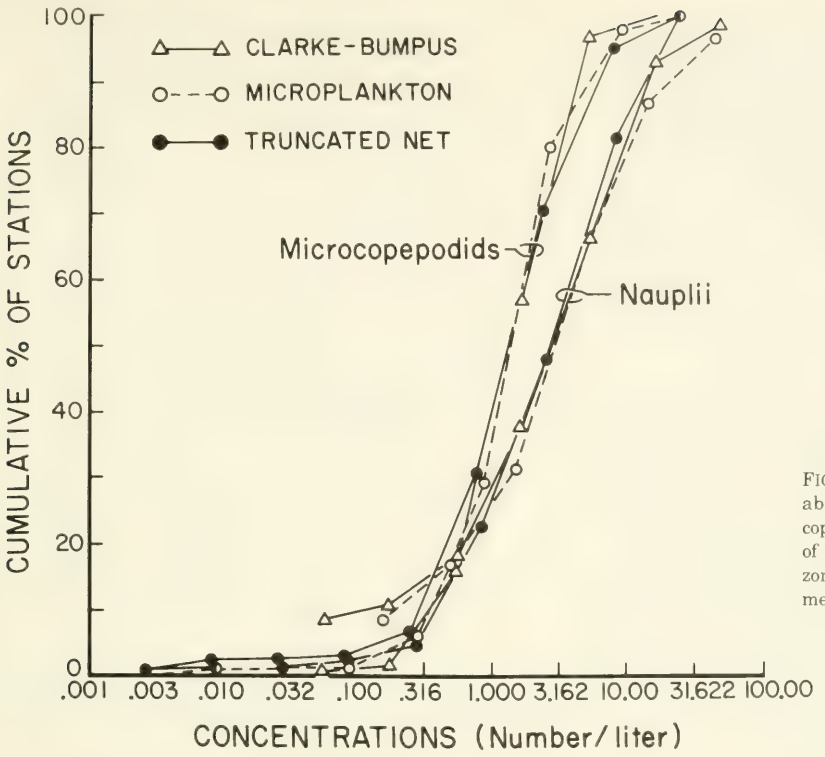

FIGURE 8.—Comparison of ogives for abundance of nauplii and microcopepodids for all sizes retained by each of the three samplers in the onshore zone corrected for volume and escapement.

DISCUSSION

Microcopepod Size and Feeding Habits of Three Larval Fishes

Feeding habits of larvae of Pacific sardine, *Sardinops sagax*; northern anchovy, *Engraulis mordax*; and jack mackerel, *Trachurus symmetricus*, as reported by Arthur (1976), may have been associated with spawning distribution of the adult fish as well as with the distribution of microcopepods and nauplii during the years of this program. Jack mackerel spawned mainly in the offshore zone, as can be determined by comparing the *Mecynocera* boundary with the distribution of jack mackerel larvae (Anonymous 1953:36). Jack mackerel larvae first start to feed when 3.0 mm long and ingest mostly 60- to 70-μm wide (total range 50 to 200 μm) copepod nauplii. However, when they have grown to 3.5 mm their food is primarily about 125-μm wide copepodid stages of small copepod species and when 9.0 mm long they eat 250- to 450-μm wide copepodids of larger species. The quick change from nauplii to copepodids, which is facilitated by their relatively large mouths, may be related to the low nauplii/copepodid ratio of the offshore zone.

Most anchovy larvae were caught inside the *Mecynocera* boundary (Anonymous 1953:34). The more omnivorous 3.0-mm long first feeding anchovy larvae select food from the 25 to 100 μm range with little preference for any size within this range. Food size increases to 125 μm when larvae are about 4.0 mm after which, though there is some increase, food size does not increase isometrically with the increase in length of larvae. This curious slow increase in food size appears to be common to early larval stages of the genus *Engraulis*, as can be observed in food-size/larval-length graphs for Japanese anchovy, *E. japonica* (Yokota et al. 1961), Argentine anchovy, *E. anchoita* (Ciechomski 1967), Peruvian anchovy, *E. ringens* (Rojas de Mendiola 1974), and can be calculated for northern anchovy, *E. mordax*, from data presented by Berner (1959) and Arthur (1976). This lack of selecting for the largest ingestible food size may be related to the high nauplii/copepodid ratio of the inshore zone and may also account for the importance of copepod eggs in the diets of anchovy larvae as reported by the above authors except Yokota et al. (1961).

Sardines spawn near the *Mecynocera* boundary, inshore of the jack mackerel and mostly offshore of anchovy (Anonymous 1953:22), but, also, more southerly of the other two. Sardine larvae combine some feeding characteristics of jack mackerel and anchovy larvae. Food particle size of sardine larvae increases isometrically with length of larvae as in jack mackerel but is smaller for unit larval length and is composed more of copepod eggs and nauplii as in anchovy larvae.

Microcopepod Densities Influence Larval Fish Survival

Other investigations in the CalCOFI area, and in similar latitudes in Japanese waters, helped to approximate the biomass spectrum of the naupliar population. Beers and Stewart (1967) estimated numbers of various microzooplankton at five locations across the California Current. Samples were taken by pumping water through several sizes of filters from depths ranging from the surface to 105 m. Their values for copepod nauplii, averaged and integrated, are compared with the values reported herein as follows:

Mesh size	*Nauplii/ liter*	*Logrithm*	*Source*
Total no., all sizes	22.078	1.3440	Beers and Stewart
Retained by 35 μm	3.878	0.5886	Beers and Stewart
Retained by 56 μm	2.884	0.4600	This report
Retained by 103 μm	0.198	−0.7033	Beers and Stewart
Retained by 120 μm	0.095	−1.0223	This report
Retained by 143 μm	0.058	−1.2366	This report

Logarithms of the above, plotted in Figure 9, are highly correlated with mesh size for the two individual sets of data as well as when they are combined. The line in Figure 9 is a least square fit to all data points combined and is expressed as:

$$N = -0.0188w + 1.3370 \quad \text{(intercept at size 0)} \qquad (1)$$

where N is concentration of nauplii (number per liter) and w is mesh aperture size. The correlation coefficient, r, is 0.9931 and the coefficient of determination, r^2, implies that 98.62% of the variation of naupliar concentrations can be explained by mesh size alone.

Least square fits for the two individual sets of data are as follows:

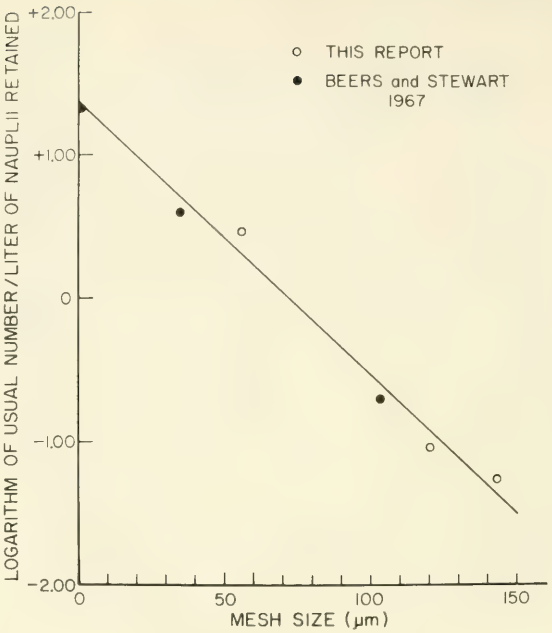

FIGURE 9.—Logarithms of the usual densities of various sizes of nauplii in relation to mesh size. The line is a least square fit to all data points combined from the equation $N = -0.0188w + 1.3370$.

Beers and Stewart

$$N = -0.01976w + 1.31857 \qquad (2)$$
$$r = 0.9994,\ r^2 = 0.9988.$$

This report

$$N = -0.02029w + 1.5577 \qquad (3)$$
$$r = 0.9900,\ r^2 = 0.9801.$$

The microcopepod assemblage in onshore water off the southern California–northern Baja California coast is strikingly similar to that in coastal waters at the same latitudes on the other side of the Pacific. Yokota et al. (1961) measured widths and lengths of 8,839 copepod nauplii and 1,389 copepodids from 666 samples captured in 1-liter containers from an area off the southeast coast of Kyushu over a 2-yr period. Average widths and lengths of nauplii were 67.7 and 156.1 μm, respectively, with a length to width ratio of 2.306. Assuming a cylindrical form, the average Kyushu nauplius has a volume of about 562,000 μm^3 which differs by only about 10% from the 510,000 μm^3 volume of the average La Jolla nauplius (Beers and Stewart 1970). Concentrations ranged from 0 to 524 nauplii/liter (only two samples were greater than 100/liter) with an

average of 13.27/liter. Size distribution as calculated from the data of Yokota et al. (1961) is:

Width of nauplii	*Average number/liter*
All sizes	13.27
>50 μm	3.87
>100 μm	0.53
>150 μm	0.10
>200 μm	0.05

In comparing the Kyushu to the California area it appears that there are fewer very small nauplii but about twice as many larger nauplii. These differences may result from the Kyushu samples being taken at the surface whereas the California samples were collected at varying depths.

Usual densities of total nauplii and copepodids of all sizes calculated from the several investigations discussed herein are as follows:

Nauplii/ liter	*Copepodids/ liter*	*Source*
36.12	1.41	This report, Equation (3)
13.27	2.10	Averaged from Yokota et al. 1961
22.08	36.35	Averaged from Beers and Stewart 1967
34.33	4.17	Averaged from Beers and Stewart 1970

The calculated number of nauplii of all sizes from this report appears to be somewhat high which may result from being derived by extrapolating from Equation (3). The average number of copepodids found by Beers and Stewart (1967) appeared to be much higher than the other investigations and may be a result of sampling an unusually rich but short-lived condition (all samples were taken during a 7-day period). Numbers of nauplii and copepodids of Beers and Stewart (1970) should be somewhat higher than the average for coastal areas because they were taken very close to the beach. In general, the usual densities in onshore areas at these latitudes (30°–35°N) is about 1.5 to 4 copepodids/liter and about 13 to 30 nauplii/liter. These densities are similar to those found by Allen (1939) who, while studying phytoplankton off California by trapping 5-liter samples, found that the combined densities of nauplii and copepodids ranged from 10 to 30/liter. Copepod nauplii average about 20–30/liter in Japanese coastal waters and 10 or less/liter in the warm offshore Kuroshio (Honjo et al.[3,4]).

These densities are considerably lower than those usually reported to be required to support growth of marine teleost larvae in the laboratory as is illustrated by a few examples. O'Connell and Raymond (1970) found poor survival of anchovy larvae in densities of nauplii and copepodids of less than 4,000/liter. Hunter (in press) used 100,000 *Gymnodinum*/liter combined with 8,000 to 115,000 rotifers/liter to grow early anchovy larvae. Houde (1975) found best survival of larval sea bream, *Archosargus rhomboidalis*, was on 50- to 100-μm wide nauplii and copepodids in densities of 1,500–3,000/liter, but 10% survived at 100/liter at low larval stock densities. In coastal and offshore areas even the highest densities of nauplii reported do not equal those used in most laboratory rearing experiments. The highest concentration of larger than 56-μm nauplii I encountered was 17.28/liter which indicates that, calculating from Equation (1), for nauplii of all sizes there were about 195/liter. Highest concentrations reported by others are 524/liter (Yokota et al. 1961), 180/liter (Beers and Stewart 1970), and 134/liter (Allen 1939).

Gallagher and Burdick (1970) calculated that the mean distance $\bar{R}$, between a particle and its nearest neighbor in a random three-dimensional array can be computed from $\bar{R} = 0.553960\rho^{-1/3}$, where ρ is their mean density in space. At concentrations of 25 nauplii/liter the distance from the mouth of a fish larva to the nearest nauplius is on the average about 18.9 mm, whereas at 200 nauplii/liter this distance is 9.5 mm.

Concentrations approaching laboratory requirements are encountered in localized conditions, i.e., Schnack (1974) caught nauplii with a 55-μm net in numbers up to 917/liter in a shallow fjord off the western Baltic. Lasker (1975) found the dinoflagellate, *Gymnodinum splendens*, in the ocean in high enough densities (20,000–40,000/liter) to support life of early laboratory-spawned anchovies. These densities were dependent on stable oceanic conditions which were quickly dispersed by a storm.

The reason for the disparity between the observed naupliar densities in the ocean and the

[3]Honjo, K., T. Kidechi, and H. Suzuki. 1959. On the food distribution and survival of post larval iwashi-I-Distribution of food organisms, the food of the anchovy and ecologically related species along the southwestern Pacific coast of Honshu, Sept.–Nov. 1958. Reports on the major coastal fish investigations, and the investigations for forecasting of oceanographic conditions and fisheries (Preliminary Report), February 1959, 7 p. Engl. transl. by S. Hayashi.

[4]Honjo, K., T. Kitachi, and M. Kudo. 1957. Food of the post-larvae of iwashi. Reports of the major coastal fish investigations for 1956 (Preliminary Report) November 1957, 5 p. Engl. transl. by S. Hayashi.

densities required for larval survival in the laboratory may be that present microplankton sampling techniques do not detect small but dense aggregations of nauplii which, however, can be found by fish larvae. It, also, may be that present rearing techniques do not approximate oceanic conditions sufficiently to permit assaying of actual prey concentrations required to allow significant larval survival. Blaxter (1965) reported that the condition factor of herring larvae living in the ocean is worse than that of larvae which died presumably of starvation in the laboratory. This may attest to greater ability of larvae to survive poor rations in the usual oceanic environment than in the laboratory.

Maximum of Naupliar Biomass Spectrum

The abundance of copepod nauplii decreases exponentially with increasing size of individuals (Figure 9), whereas the volume of an individual nauplius increases exponentially with increasing size (roughly by the cube of width). When the naupliar size range is divided into 10-μm wide size classes and the average volume per nauplius is multiplied by numbers of individuals per class (calculated from the equation for combined data, Figure 9) it is seen that the naupliar biomass is at a maximum at about the 70 μm width (Figure 10) even though there are many more nauplii of smaller sizes.

Figure 10 includes, also, the food-particle size range at first feeding of larvae of Pacific sardine, northern anchovy, and jack mackerel (Arthur 1976). It is interesting to note that these ranges overlap at the 50- to 80-μm width range which brackets the naupliar biomass spectrum maximum. This suggests that larval feeding habits of these three fishes have evolved to take advantage of this important food resource at first feeding.

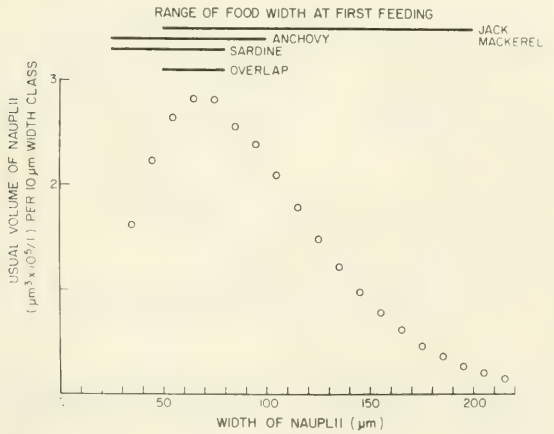

FIGURE 10.—Biomass spectrum of naupliar size range compared with food size at first feeding of the larvae of three fishes in the California Current system.

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ABUNDANCE AND POTENTIAL YIELD OF THE SCALED SARDINE, *HARENGULA JAGUANA*, AND ASPECTS OF ITS EARLY LIFE HISTORY IN THE EASTERN GULF OF MEXICO[1]

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ABSTRACT

Eggs and larvae of the scaled sardine, *Harengula jaguana*, were collected in 1971–74 from the eastern Gulf of Mexico to determine spawning seasons, spawning areas, adult biomass, and fisheries potential. Aspects of the early life history of the species also were studied. Spawning occurred from January to September, but was most intense from May to August, when surface temperatures ranged from 20.8° to 30.7°C and surface salinities were 29.9 to 36.9‰. All spawning occurred between the coast and the 30-m depth contour, mostly within 50 km of the coast. The biomass of scaled sardines, based on annual spawning estimates, apparently increased from 1971 to 1973, the mean estimate for the 3 yr being 184,527 metric tons. Potential yield estimates, based on the 3-yr mean biomass, ranged from 46,000 to 92,000 metric tons. Larval abundance and mortality rates were estimated from 1973 data. More than 99.9% mortality occurred between time of spawning and attainment of 15.5 mm standard length at 20 days of age. Comparisons were made of scaled sardine distribution, abundance, potential yield, and larval mortality with those of other eastern Gulf clupeids.

Scaled sardine, *Harengula jaguana* Poey, is abundant in coastal waters of the western Atlantic from New Jersey to Santos, Brazil, including the Gulf of Mexico (Berry 1964). It is common from Florida to Brazil (Rivas 1963), but there are no large-scale directed fisheries for the species. Klima (1971) reported it to be an abundant, surface-schooling species that is usually found within the 20-fathom curve in the northeastern Gulf of Mexico. It is one of the most common species in Gulf Coast estuaries (Gunter 1945; Springer and Woodburn 1960; Roessler 1970). Because of its abundance, it is an important latent fishery resource in the Gulf of Mexico and Caribbean region (Reintjes and June 1961; Bullis and Thompson 1970; Klima 1971). Small catches of *Harengula* spp. totalling 2,189 metric tons in 1974 presently are landed by Cuba, Brazil, and the Dominican Republic (Food and Agriculture Organization 1975). No reported catches are made by the United States, but a small amount, probably less than 500 tons annually, is landed in Florida for bait in commecial and recreational fishing.

Some aspects of the biology of scaled sardines are known. Low (1973) discussed the species and its occurrence in Biscayne Bay, Fla., including food habits and juvenile growth rates. Fecundity, size at maturity, and spawning were reported by Martinez and Houde (1975). Roessler (1970) discussed growth, recruitment, and the relationship of environmental factors to scaled sardine abundance in an Everglades estuary, and Springer and Woodburn (1960) discussed its ecology in Tampa Bay. Eggs and larvae have been described by Matsuura (1972), Houde and Fore (1973), Houde et al. (1974), and Gorbunova and Zvyagina (1975).

Objectives of this study were to estimate scaled sardine biomass and fishery potential in the eastern Gulf of Mexico from the distribution and abundance of its eggs and larvae. Information on the early life history also was obtained. Similar studies on round herring, *Etrumeus teres*, and thread herring, *Opisthonema oglinum*, were recently published (Houde 1976, 1977a, b).

METHODS

Methods to determine scaled sardine biomass and fisheries potential are the same as those used for round herring and thread herring (Houde 1977a, b). Collecting methods were described (Houde 1977a), and summarized station data from

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the 17 ichthyoplankton cruises have been published (Houde and Chitty 1976; Houde et al. 1976). The survey area and its potential sampling stations were illustrated in figure 1 of Houde (1977a, b). Analytical and statistical procedures are based on those discussed by Saville (1964), Ahlstrom (1968), and Smith and Richardson (in press).

RESULTS AND DISCUSSION

Occurrence of Eggs and Larvae

A total of 19,183 scaled sardine eggs and 3,828 larvae were collected during the 17 cruises, in which 867 stations were sampled. Scaled sardines composed 59.8% of all clupeid eggs collected and their larvae composed 13.2% of all clupeid larvae. Scaled sardine eggs made up 6.3% of the total fish eggs from the 867 stations and their larvae constituted 2.7% of the total larval fish catch.

Scaled sardine eggs or larvae were collected on cruises from January through September, but they were most abundant from May through August (Table 1). Stations where they occurred are given in Figure 1. Distribution and abundance of eggs and larvae are illustrated for the May through August cruises (Figures 2–5). Spawning from January to March probably is confined to the southernmost parts of the survey area, since eggs and larvae were collected only at stations south of lat. 26°N on cruises during those months.

No eggs were collected where depths exceeded 30 m (Figure 1). Larval distributions were similar to those for eggs, except for a single anomalous occurrence of larvae at a station on the 200-m depth contour (Figures 1, 3). On cruises CL7405 and CL7412 several stations nearer to shore (of only 4–10 m depth) than any on previous cruises were sampled (Figure 5). On cruise CL7412, when intense spawning was taking place, catches of eggs at the nearshore stations exceeded catches at the regular stations. Mean egg abundance under 10 m^2 at positive stations was 1.85 times greater at the nearshore stations than at the regular stations (158.93 compared with 85.75). Log_{10} transformed means were tested in a t-test.

Stations	*No. of stations with scaled sardine eggs*	Log_{10} *mean*	Log_{10} $S_{\bar{x}}$
Regular	9	1.0056	0.3343
Nearshore	11	1.8118	0.1913

$t_{calc} = 2.15^*$ $\quad t_{0.05(2)18} = 2.10$

Differences were significant ($P<0.05$). Failure to sample nearshore stations on earlier cruises probably resulted in an underestimate of scaled sardine spawning and also an underestimate of adult biomass if egg distribution during cruise CL7412 was representative of earlier cruises.

The observed egg and larvae distributions indicate that most adults are located where depth

TABLE 1.—Summarized data on cruises to the eastern Gulf of Mexico, 1971–74, to estimate abundance of scaled sardine eggs and larvae. GE = RV *Gerda*, 8C = RV *Dan Braman*, TI = RV *Tursiops*, 8B = RV *Bellows*, IS = RV *Columbus Iselin*, *CL* = RV *Calanus*.

Cruise	Dates	Number of stations	Positive stations for eggs[1]	Positive stations for larvae[2]	Mean egg abundance under 10 m^2		Mean larvae abundance under 10 m^2	
					All stations	Positive stations	All stations	Positive stations
GE7101[3] 8C7113	1–8 Feb. 1971	20	1	0	0.64	23.05	0.00	0.00
TI7114	7–18 May 1971	123	2	12	0.78	64.66	6.73	51.52
GE7117 8C7120	26 June–4 July 1971	27	2	0	1.67	19.95	0.00	0.00
TI7121 TI7131 8B7132	7–25 Aug. 1971	146	8	6	0.83	28.09	0.21	4.37
GE7127 8B7201	7–16 Nov. 1971	66	0	0	0.00	—	0.00	—
GE7202	1–11 Feb. 1972	30	0	0	0.00	—	0.00	—
GE7208	1–10 May 1972	30	1	4	1.68	76.21	1.24	11.57
GE7210	12–18 June 1972	13	3	3	35.31	146.94	5.97	22.78
IS7205	9–17 Sept. 1972	34	0	2	0.00	—	0.16	4.70
IS7209	8–16 Nov. 1972	50	0	0	0.00	—	0.00	—
IS7303	19–27 Jan. 1973	51	0	1	0.00	—	0.01	0.26
IS7308	9–17 May 1973	49	8	14	14.38	154.16	9.26	38.34
IS7311	27 June–6 July 1973	51	6	6	31.59	174.14	0.59	5.51
IS7313	3–13 Aug. 1973	50	9	11	67.49	747.09	10.86	50.26
IS7320	6–14 Nov. 1973	51	0	0	0.00	—	0.00	—
CL7405	28 Feb.–9 Mar. 1974	36	0	4	0.00	—	0.39	4.06
CL7412	1–9 May 1974	44	20	23	50.29	125 82	14.45	28.79

[1]Positive station is a station at which scaled sardine eggs were collected.
[2]Positive station is a station at which scaled sardine larvae were collected.
[3]An ICITA 1-m plankton net was used on this cruise. On all other cruises a 61-cm bongo net was used.

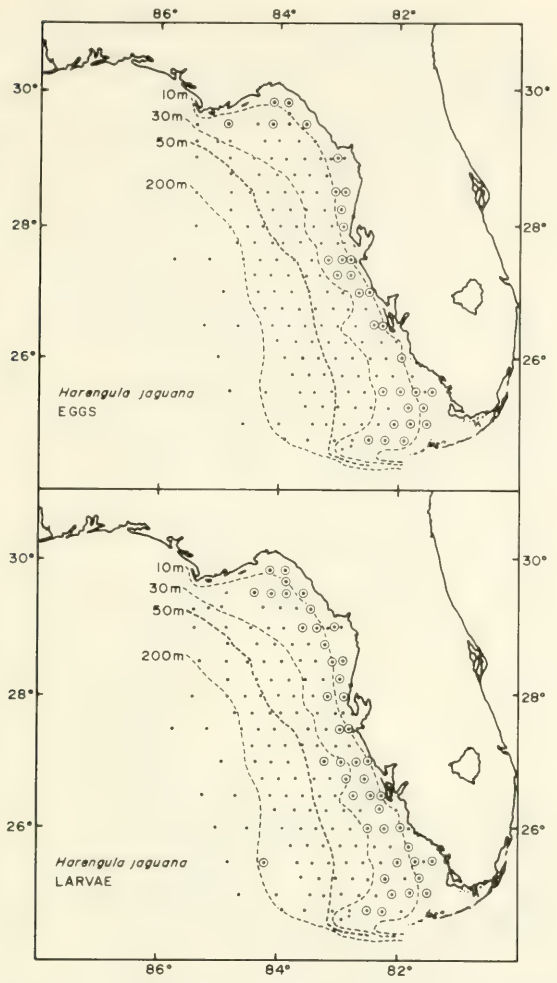

FIGURE 1.—Top. Stations in the survey area where eggs of scaled sardines were collected at least once during 1971–74. Stations where eggs did not occur are indicated by dots. Bottom. Stations in the survey area where larvae of scaled sardines were collected at least once during 1971–74. Stations where larvae did not occur are indicated by dots.

is <20 m and that nearly all are found within the 30-m depth contour. Spawning adults are confined to a band within 85 km of the coast. Klima (1971) reported that scaled sardines in the Gulf of Mexico usually are found within the 20-fathom curve (36.5 m), but he noted occasional occurrence over depths as great as 165 fathoms (302 m). Brazilian scaled sardines also spawned near the coast, within 18.5 km of shore where water depth was <65 m (Matsuura 1972).

There were no areas in the eastern Gulf where consistently high egg or larval catches occurred that would suggest great concentrations of adults. Consistent catches of eggs and larvae between lat. 24°45′N to 25°45′N and long. 81°30′W to 82°30′W, as well as just north of Tampa Bay between lat. 28°00′N to 28°30′N and long. 82°45′W to 83°15′W did indicate that scaled sardines usually were abundant in those areas.

Mean egg abundances for the 17 cruises ranged from 0.00 to 67.49 under 10 m^2 of sea surface (Table 1). Considering only positive stations, means ranged from 19.95 to 747.09 under 10 m^2 (Table 1). Abundances of eggs at stations rarely exceeded 100 under 10 m^2 of sea surface during 1971 and 1972, but frequently were between 100 and 1,000 under 10 m^2 during 1973 and 1974 (Figures 2–5). Only once, in August 1973, did abundance of eggs exceed 1,000 under 10 m^2 (Figure 4).

Cruise means for scaled sardine larval abundances ranged from 0.00 to 14.45 under 10 m^2 when all stations were considered, and from 0.26 to 51.52 under 10 m^2 at positive stations (Table 1). At positive stations larval abundances usually ranged from 11 to 100 under 10 m^2, and exceeded 100 under 10 m^2 at only eight stations during 1971–74 (Figures 2–5).

Most scaled sardine eggs and larvae were found nearer to shore than those of either thread herring or round herring (Houde 1977a, b). However, there was considerable overlap in areas and seasons of occurrence of thread herring and scaled sardine spawning. Eggs and larvae of scaled sardines and round herring did not occur together because round herring did not spawn in water shallower than 30 m, and most spawning by that species occurred during winter.

Temperature and Salinity Relations

Scaled sardine eggs were collected at surface temperatures from 20.8° to 30.7°C and at surface salinities from 29.92 to 36.88‰. Larvae ≤5 mm standard length (SL), 5 days or less in age, were taken at surface temperatures from 18.4° to 30.5°C and surface salinities of 27.27 to 36.88‰. Vertical sections showing temperature and salinity profiles for cruises during the scaled sardine spawning season indicated that surface temperatures differed from those at 10 m by a maximum of only 1°C, but that a maximum difference of 4°C could occur at 30 m. The difference between the surface and the 30-m depth usually did not exceed 2°C. Salinity differences between the surface and 10 m were always <0.5‰ and never exceeded 1.5‰

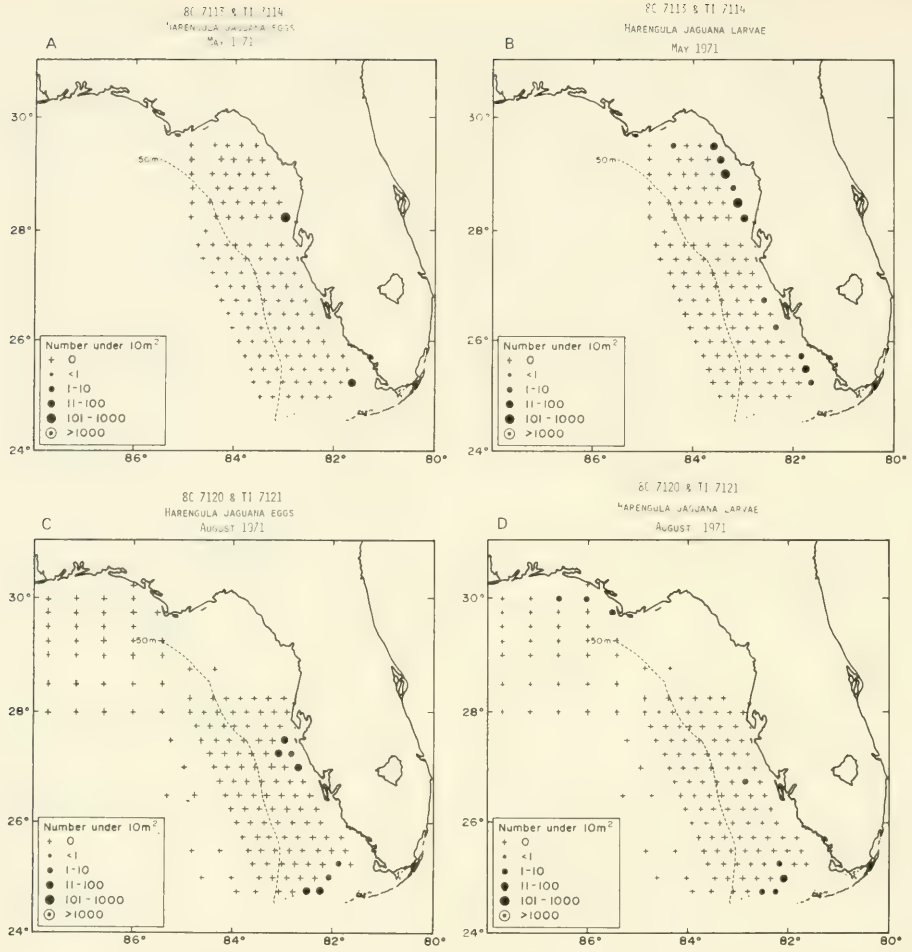

FIGURE 2.—Distribution and abundance of scaled sardine eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B. Cruise 8C7113–TI7114, May 1971. C, D. Cruise 8C7120–TI7121, August 1971.

between the surface and 30 m. The buoyant eggs and pelagic larvae probably developed at temperatures and salinities similar to those at the sea surface.

Relatively few eggs or ≤5.0-mm larvae occurred where surface temperature was <24.0°C over the 1971–74 period (Figure 6). For eggs, 82.3% of the station occurrences were at surface temperatures above 24°C; for larvae, 71.0% occurred above 24°C. Although spawning occurred over a wide salinity range, 71.0% of the stations with eggs had salinities that exceeded 35.0‰; 62.3% of the stations with ≤5.0-mm larvae had salinities above 35.0‰.

Matsuura (1972) collected eggs and larvae of Brazilian scaled sardine at temperatures and salinities within the ranges observed for eggs and larvae in the eastern Gulf. Spawning occurred at temperatures and salinities similar to those recorded for thread herring (Houde 1977b). Scaled sardine eggs and larvae were found over slightly wider ranges of temperature and salinity than were thread herring, reflecting the slightly longer spawning season of scaled sardines in the eastern Gulf and their tendency to be most abundant nearer to the coast where temperatures and salinities varied most.

Egg and Larval Abundance in Relation to Zooplankton

There was no apparent relationship between either egg or larval abundance at stations and

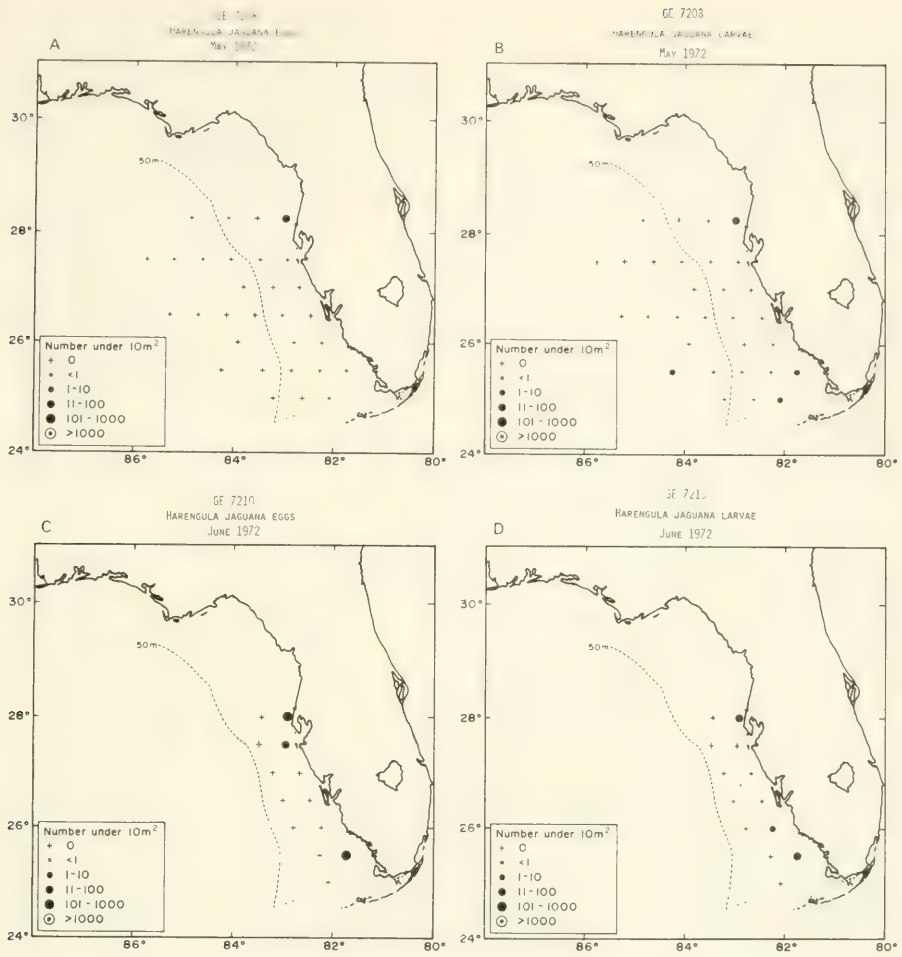

FIGURE 3.—Distribution and abundance of scaled sardine eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B. Cruise GE7208, May 1972. C, D. Cruise GE7210, June 1972.

volume of zooplankton collected in the 333-μm mesh bongo net in 1972–74. Mean zooplankton volume was 153.4 cm³/1,000 m³ in 1972–74 (Houde and Chitty 1976). Highest abundances of scaled sardine eggs and larvae occurred where zooplankton volumes exceeded 153.4 cm³/1,000 m³ but correlations between zooplankton volume and scaled sardine egg or larval abundance were not significant. Because the 333-μm mesh did not collect small copepod nauplii, a major food of fish larvae, and because zooplankton was not identified, significant correlations between larvae and zooplankton were unlikely. The relatively high catches of eggs at stations with high zooplankton volumes may have reflected the ability of scaled sardine adults to concentrate in rich zooplankton areas, rather than indicating that eggs were spawned where food would be abundant for larvae.

Relative Fecundity and Size at Maturity

Mean relative fecundity of scaled sardines is 528.0 ova/g ($S_{\bar{x}}$ = 26.5 ova/g), based on data from 22 females collected near Miami, Fla., by Martinez and Houde (1975). They found that two modal groups of ova ripened during the spawning season and that both modes apparently were spawned. The relative fecundity estimate here differs slightly from their reported value because they estimated it for female weights minus ovary weights. To determine stock biomass, the best

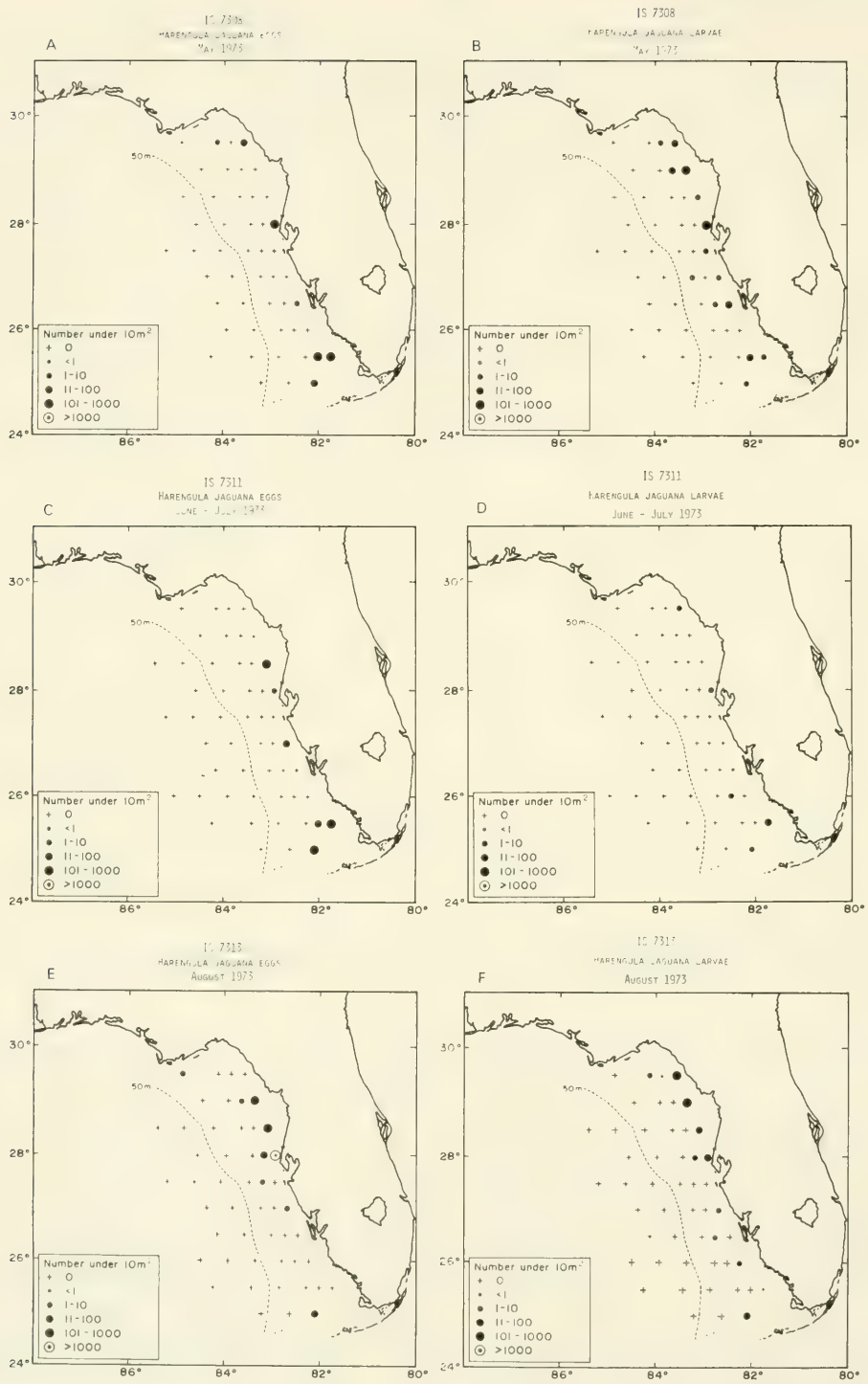

FIGURE 4.—Distribution and abundance of scaled sardine eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B. Cruise IS7308, May 1973. C, D. Cruise IS7311, June–July 1973. E, F. Cruise IS7313, August 1973.

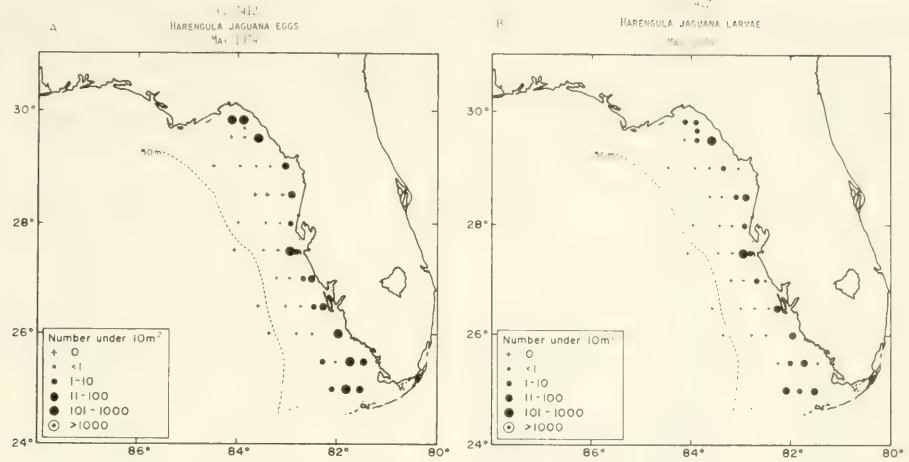

FIGURE 5.—Distribution and abundance of scaled sardine eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B. Cruise CL7412, May 1974.

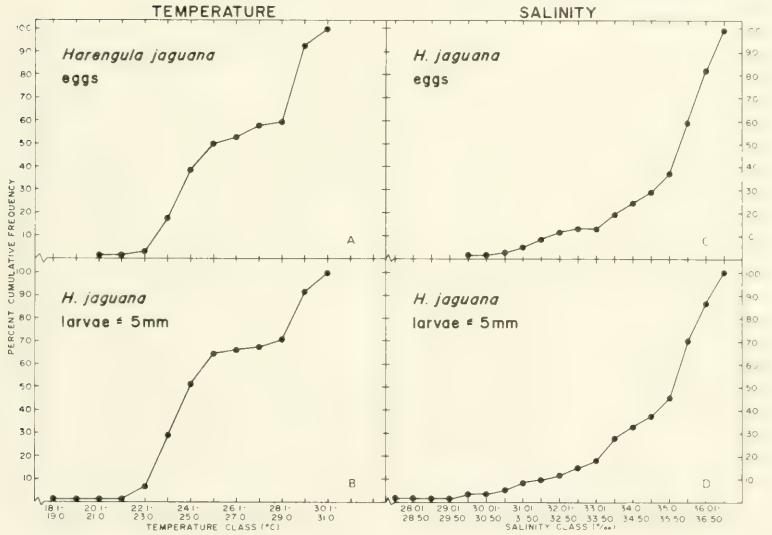

FIGURE 6.—Percent cumulative frequency distribution of 1971–74 stations where scaled sardine eggs occurred in relation to surface temperatures (A) and to surface salinities (C), and ≤5.0-mm SL larvae occurred in relation to surface temperatures (B) and surface salinities (D).

relative fecundity estimate is for total weight, including ovary and the estimate given here is based on that criterion. Because relative fecundity did not differ significantly among females from 8.5 to 16.3 cm SL (14.8 to 98.4 g) (Martinez and Houde 1975), the mean value was used in calculating biomass estimates. Mean relative fecundity with 0.95 confidence limits is 528.0 ± 55.1 ova/g. It seems unlikely that biomass estimating errors greater than ±10% could be attributable to errors in fecundity estimates.

Cruise Egg Abundance

The estimated abundances of scaled sardine eggs, before correction for egg stage duration, within the areas represented by each of the cruises range from 0.00 to 103.39 × 10^{10} (Table 2). The Table 2 estimates, which represent the number of eggs present on a day during a cruise, were corrected for egg stage duration and then expanded to represent the number of days encompassed by the cruise period (Sette and Ahlstrom 1948; Houde 1977a), before they were used in the biomass estimating procedure.

Time Until Hatching

Egg stage duration is less than 24 h for scaled sardines when temperatures are above 24°C.

TABLE 2.—Abundance estimates of scaled sardine eggs for each cruise. Estimates were obtained using equations (2) and (3) (Houde 1977a) and are not corrected for duration of the egg stage.

Cruise	Area represented by the cruise ($m^2 \times 10^9$)	Positive area[1] ($m^2 \times 10^9$)	Cruise egg abundance (eggs $\times 10^{10}$)
GE7101	25.79	0.77	0.18
8C7113 and TI7114	120.48	18.32	0.94
GE7117	101.10	7.93	1.69
8C7120 and TI7121	189.43	13.41	1.57
GE7127, 8B7132 and TI7131	72.99	0.00	0.00
8B7201 and GE7202	148.85	0.00	0.00
GE7208	124.88	27.56	2.51
GE7210	48.43	15.60	17.10
IS7205	104.59	4.88	0.00
IS7209	149.80	0.00	0.00
IS7303	149.80	3.05	0.00
IS7308	151.42	43.38	21.77
IS7311	156.50	25.43	49.44
IS7313	153.18	40.79	103.39
IS7320	153.89	0.00	0.00
CL7405	52.00	5.84	0.00
CL7412	91.33	43.45	45.93

[1]Positive area is defined as the area representing stations where either eggs or larvae of scaled sardines were collected.

Newly fertilized eggs were collected only at night in the Gulf of Mexico surveys and only advanced embryos usually were present from midday to late afternoon. Similar observations were made for scaled sardine eggs collected near Miami and used in laboratory rearing experiments (Houde and Palko 1970; Houde et al. 1974). The estimated peak spawning time is 2200 h.

Egg abundance was underestimated on most cruises because hatching time was less than 1 day. All cruise abundances were adjusted by dividing them by the estimated mean egg stage duration (Table 3) before annual spawning estimates were made.

Adjusting Cruise Egg Abundance Estimates for Area

Some cruises did not completely cover the area within the 30-m depth contour of the eastern Gulf where scaled sardines spawned. Egg abundance estimates for those cruises were adjusted by dividing the cruise abundance estimate (Table 2) by an adjustment factor, the proportion of the spawning area represented by the cruise. Egg abundance estimates were adjusted for cruises GE7117, 8C7120–TI7121, GE7208, and GE7210. Area adjustment factors were: GE7117—0.394; 8C7120–TI7121—0.746; GE7208—0.644; and GE7210—0.574. Cruise IS7205, in which scaled sardine larvae but no eggs were taken, also did not encompass the entire spawning area. Larval abundance estimates were adjusted for that cruise by its area factor, 0.750. Cruise egg abundance estimates from Table 2, after adjustment, were: GE7117—4.29×10^{10}; 8C7120–TI7121—2.10×10^{10}; GE7208—3.90×10^{10}; and GE7210—29.79×10^{10}.

TABLE 3.—Assigned egg stage durations of scaled sardine eggs for each cruise in which they occurred, 1971–73.

Cruise	Egg stage duration (days)	Cruise	Egg stage duration (days)
GE7101	1.17	GE7208	0.84
8C7113		GE7210	0.80
TI7114	0.84	IS7308	0.84
GE7117	0.80	IS7311	0.80
8C7120		IS7313	0.80
TI7121	0.80		

Annual Spawning and Biomass Estimates

Method I

Estimates of total annual spawning by scaled sardines were obtained after egg stage duration and area factor corrections had been made on daily spawning estimates using the Sette and Ahlstrom (1948) method and procedures described by Houde (1977a). They were: 44.106×10^{11} eggs in 1971, 391.357×10^{11} eggs in 1972, and $1{,}025.834 \times 10^{11}$ eggs in 1973 (Table 4). No estimate was obtained in 1974 because the entire season was not surveyed, but the abundance of eggs from cruise CL7412 (Table 2) suggested that annual spawning was high in that year.

Estimated biomasses increased from 16,708 metric tons in 1971 to 148,255 metric tons in 1972, and to 388,610 metric tons in 1973 (Table 4). Variance estimates for each year's spawning (Table 4) were used to place 0.95 confidence intervals on biomass estimates. These ranged from 0 to 56,210 metric tons in 1971, 0 to 327,130 metric tons in 1972, and 300,965 to 476,271 metric tons in 1973. The mean of the three annual biomass estimates was 184,527 metric tons. The 1972 estimate may be unreliable because of poor area coverage and curtailment of cruise GE7210 due to a hurricane, but the low 1971 estimate probably is accurate because area coverage was good on cruises during the peak spawning period.

A severe red tide in 1971 occurred during spring and summer along the Florida coast of the Gulf of Mexico (Steidinger and Ingle 1972), and it may have caused a high mortality of adult scaled sardines. Dead scaled sardines were observed in red tide areas during cruise GE7117. It is also possible

TABLE 4.—Annual spawning and biomass estimates for scaled sardines from the eastern Gulf of Mexico during 1971, 1972, and 1973 spawning seasons. Estimates are based on the Sette and Ahlstrom (1948) technique. Details of the estimating procedure are given in Houde (1977a).

Year	Cruise	Daily spawning estimate (eggs × 10^{11})	Days represented by cruise	Eggs spawned during cruise period (× 10^{11})	Variance estimates on spawned eggs (× 10^{24})	Adult biomass (metric tons)
1971	GE7101	0.015	51.5	0.773	0.134	
	8C7113					
	TI7114	0.112	74.5	8.344	1.950	
	GE7117	0.541	44.5	24.074	22.959	
	8C7120					
	TI7121	0.263	41.5	10.915	2.121	
Annual total				44.106	27.164	16,708
1972	8B7201					
	GE7202	0.000	50.0	0.000	—	
	GE7208	0.468	65.0	30.420	22.664	
	GE7210	3.721	97.0	360.937	534.743	
Annual total				391.357	557.407	148,255
1973	IS7303	0.000	63.5	0.000	—	
	IS7308	2.613	79.5	207.734	56.388	
	IS7311	6.180	43.5	268.830	42.829	
	IS7313	12.924	42.5	549.270	34.628	
Annual total				1,025.834	133.845	388,610

that few adult scaled sardines were killed, but that they did not spawn during red tides or that spawned eggs experienced high mortality. Failure to spawn or unusual egg mortality could have caused biomass to be underestimated in that year.

Effects on biomass estimates of area adjustments for the four cruises that did not completely cover the scaled sardine spawning area were important. Unadjusted biomass in 1971 was only 10,100 metric tons, 60.5% of the adjusted estimate; in 1972 it was 85,964 metric tons, 58.0% of the adjusted estimate.

Method II

Biomass estimates, using Simpson's (1959) method in a modified form (Houde 1977a), were calculated (Table 5). Mean biomass estimated for the 3 yr was 146,595 metric tons.

TABLE 5.—Annual spawning and biomass estimates for scaled sardines from the eastern Gulf of Mexico during 1971, 1972, and 1973. Estimates are based on the method described by Simpson (1959).

Year	Cruise	Daily spawning estimate (eggs × 10^{11})	Annual spawning estimate (eggs × 10^{11})	Adult biomass (metric tons)
1971	GE7101	0.015		
	8C7113			
	TI7114	0.112		
	GE7117	0.541		
	8C7120			
	TI7121	0.263		
			42.981	16,282
1972	8B7201			
	GE7202	0.000		
	GE7208	0.468		
	GE7210	3.721		
			245.940	93,168
1973	IS7303	0.000		
	IS7308	2.613		
	IS7311	6.180		
	IS7313	12.924		
			872.000	330,334

Most Probable Biomass

Scaled sardines as small as 8.0 cm SL are mature (Martinez and Houde 1975), and estimates of adult biomass from egg and larvae surveys probably include most of the stock, juvenile weights being relatively insignificant. Biomass estimates ranged from 16,000 to nearly 400,000 metric tons and stock apparently increased from 1971 to 1973. The evidence from cruise CL7412 indicated that spawning increased nearer to shore than measured at regular survey stations. This suggests that biomasses were underestimated, perhaps by as much as 30%. If so, then biomass may have ranged from 23,000 to 571,000 metric tons during 1971–73, the mean being 265,000 metric tons. Despite variability in estimates, it is clear that the eastern Gulf scaled sardine stock was less than 700,000 metric tons between 1971 and 1973, and it apparently was less than 100,000 metric tons in 1971.

Comparison of Scaled Sardine Biomass With That of Other Clupeids

Biomass of scaled sardines in the eastern Gulf of Mexico is similar to that reported for round herring and thread herring (Houde 1977a, b). Mean biomass of round herring was estimated to be approximately 400,000 metric tons, mostly distributed between the 30- and 200-m depth contours, while thread herring mean biomass was about 250,000 metric tons, much of it occurring in the same areas as scaled sardine, although

many thread herring also occurred farther offshore (Houde 1977b). In aggregate the three species totalled approximately 850,000 metric tons. The menhaden (*Brevoortia* spp.) resource apparently is small in the survey area, since relatively few eggs and larvae were collected (Houde et al. 1976). No estimate of Spanish sardine (*Sardinella* spp.) biomass was obtained, but its eggs and larvae were abundant (Houde et al. 1976). Its biomass may be as great as that for thread herring, i.e., 250,000 metric tons. If true, then aggregate adult biomass of unfished clupeids exceeds 1 million metric tons. The contention that large potential fisheries exist in the eastern Gulf of Mexico is supported by the estimated biomasses. However, none of the individual species appears to represent a resource as large as that of Gulf menhaden, *B. patronus,* which presently yields about 500,000 metric tons annually to the northern Gulf fishery.

Concentration of Biomass

Scaled sardine eggs and larvae occurred in most of the 76 $\times$ 10^9 m^2 area between the coast and 30-m depth contour, except for approximately 15 to 20 $\times$ 10^9 m^2 in the northeastern part of the survey area (Figure 1). During the spawning season, adult scaled sardines were assumed to occur in 60 $\times$ 10^9 m^2 of the eastern Gulf. Concentration of biomass, assuming an even distribution, based on the annual biomass estimates from Method I (Table 4) and their 0.95 confidence limits were: 1971, 0 to 9.4 kg/ha; 1972, 0 to 54.5 kg/ha; and 1973, 50.2 to 79.4 kg/ha. Mean biomass concentrations were: 1971, 2.8 kg/ha; 1972, 24.7 kg/ha; and 1973, 64.8 kg/ha. Estimated scaled sardine biomasses under a hectare of sea surface are similar to those of thread herring but less than those of round herring (Houde 1977a, b).

Potential Yield to a Fishery

Estimates of annual yield varied greatly from year to year, reflecting the biomass fluctuations (Table 6). The estimator $C_{max} = XMB_0$ was used to predict potential maximum sustainable yield (Alverson and Pereyra 1969; Gulland 1971, 1972). X is assumed to equal 0.5 and B_0 is the virgin biomass. M, the natural mortality coefficient, was allowed to vary from 0.5 to 1.0, values that are probable for scaled sardines. The range of potential yields over the 3-yr period was 4,177 to 194,305 metric tons (Table 6). Based on mean biomass estimates for 1971–73, potential yield was between 46,132 and 92,264 metric tons. If scaled sardines were evenly distributed over the 60 $\times$ 10^9 m^2 where they occur in the eastern Gulf, harvestable annual yield, based on 1971–73 mean biomass, is 7.7 to 15.4 kg/ha.

TABLE 6.—Range of potential yield estimates for eastern Gulf of Mexico scaled sardines, based on biomass estimates in 1971, 1972, and 1973 by the Sette and Ahlstrom (1948) method. Yields are predicted at three possible values of M, the natural mortality coefficient. Biomass estimates were obtained from values in Table 4.

Year	Biomass estimate (metric tons)	Estimated potential annual yields (metric tons) for given values of M		
		M=0.50	M=0.75	M=1.0
1971	16,708	4,177	6,266	8,354
1972	148,255	37,064	55,596	74,128
1973	388,610	97,153	145,729	194,305
Mean of 3 yr	184,527	46,132	69,198	92,264

Comparison of Potential Yield With That of Other Clupeids

Potential yield of scaled sardines is slightly less than that estimated for thread herring and less than that for round herring (Houde 1977a, b). Using mean annual biomass estimates by Method I, and the value 1.0 for M, potential maximum sustainable yields are: scaled sardines—92,264 metric tons; thread herring—120,598 metric tons; and round herring—212,238 metric tons. Total potential for the three species is 425,100 metric tons. If Spanish sardines are as abundant as thread herring, they could contribute another 120,000 metric tons raising the aggregate potential yield to 545,100 metric tons.

Potential yields were estimated for adult stock. If a significant biomass of harvestable juveniles is present, they could contribute to the yield. For scaled sardines, and probably round herring (Houde 1977a), small size at first maturity makes it unlikely that a significant, unestimated juvenile biomass is present, but the large size at first maturity of thread herring (Prest[3]) and Spanish sardines (Varea Rivero 1967) indicates that a significant unestimated biomass of juveniles may be present.

[3]Prest, K. W., Jr. 1971. Fundamentals of sexual maturation, spawning, and fecundity of thread herring (*Opisthonema oglinum*) in the eastern Gulf of Mexico. Unpubl. manuscr., Natl. Mar. Fish. Serv., NOAA, St. Petersburg Beach, Fla.

Larval Abundance

Larval abundance varied annually and seasonally (Table 7; Figure 7); the greatest abundances being observed in 1973 and 1974 cruises. Abundance estimates for cruises in which larvae occurred, ranged from 0.20 to 16.63 $\times$ 10^{10} larvae. Estimated annual abundances of larvae were low in 1971 and 1972, but increased in 1973 (Figure 8). No annual estimates were available for 1974, but the great abundance of larvae from cruise CL7412 (Figure 7) suggests that more larvae were present in that year than in any previous year. The increases in larval abundance between 1971 and 1974 are further evidence that spawning intensity increased during the period.

Some scaled sardines as long as 30 mm SL were collected but few larvae longer than 20 mm were taken, and only larvae from 1.1 to 20.0 mm are included in the length–frequency distributions. Most larvae of 1.1 to 3.0 mm were distorted from collection and preservation. Scaled sardine larvae are 2.4 mm at hatching, but within 15 h their length increases to more than 4.0 mm, mostly due to straightening of the body axis rather than true growth (Houde et al. 1974). The most abundant larvae were 2.1 to 4.0 mm in 1972–74, but were larger in 1971 (Figure 7) when towing speed was faster (Houde 1977a) and mesh escapement by small larvae may have been greater.

The ratio of night-caught to day-caught scaled sardine larvae increased slowly as larvae increased in length. No larvae longer than 18.0 mm were sampled during daylight hours. An exponential model $R = 0.7999e^{0.0550X}$ was fitted to the data (Figure 9), where R is the ratio of night-caught to day-caught larvae and X is standard length. It provided the correction factor R, by which daytime catches were adjusted to obtain abundance estimates of larvae by 2-mm length classes in each station area (equation 11, Houde 1977a).

An exponential decrease in abundance of larvae was observed in 1973 (Figure 8) and the larval mortality rate was estimated from these data. Larvae longer than 3.0 mm were assumed to be fully vulnerable to the sampling gear. Abundances (Figure 8) were previously corrected for daytime avoidance.An exponential function was fitted to the data, and the instantaneous rate of decline in abundance per millimeter increase in length was estimated for larvae from 3.1 to 20.0 mm SL. The instantaneous coefficient, Z = 0.3829, is a measure of larval mortality, if gear avoidance was not too great for larval length classes in the analysis. The 0.95 confidence limits on Z are $Z \pm 0.0833$. The observed coefficient corresponds to a 31.8% decrease in larval abundance per millimeter increase in length. Although mortality was not estimated for 1972 larvae, the high estimated abundance of larvae longer than 10 mm (Figure 8) indicates that survival may have been relatively good in that year.

TABLE 7.—Abundance estimates of scaled sardine larvae for each cruise. Estimates include larvae in all size classes and were obtained using equations (2) and (3) (Houde 1977a).

Cruise	Area represented by the cruise ($m^2 \times 10^9$)	Positive area[1] ($m^2 \times 10^9$)	Cruise larvae abundance[2] (larvae $\times 10^{10}$)
GE7101	25.79	0.77	0.00
8C7113 and TI7114	120.48	18.32	8.11
GE7117	101.10	7.93	0.00
8C7120 and TI7121	189.43	13.41	0.39
GE7127, TI7131 and 8B7132	72.99	0.00	0.00
8B7201 and GE7202	148.85	0.00	0.00
GE7208	124.88	27.56	1.85
GE7210	48.43	15.60	2.89
IS7205	104.59	4.88	0.17
IS7209	149.80	0.00	0.00
IS7303	149.80	3.05	0.01
IS7308	151.42	43.38	14.02
IS7311	156.50	25.43	0.92
IS7313	153.18	40.79	16.63
IS7320	153.89	0.00	0.00
CL7405	52.00	5.84	0.20
CL7412	91.33	43.45	13.19

[1]Positive area is defined as the area representing stations where either eggs or larvae of scaled sardines were collected

[2]Values are not adjusted for cruises that did not encompass the entire area, nor have estimates been corrected to account for gear avoidance by larvae at stations sampled in daylight.

Mortality relative to age of larvae was determined assuming an exponential model of growth for scaled sardine larvae, based on evidence from laboratory rearing experiments. Mean daily growth increments of scaled sardine larvae reared at temperatures above 26°C exceeded 0.5 mm, and frequently were in the range of 0.7 to 1.0 mm (Houde and Palko 1970; Saksena and Houde 1972; Saksena et al. 1972). Methods to estimate age at length and mortality have been reported (Houde 1977a).

Mean egg stage duration for scaled sardine is about 0.81 day. In 1973 the nonfully vulnerable length classes were 1.1 to 3.0 mm. Duration of that larval stage is from 1.0 to 3.0 days based on laboratory experiments (Saksena and Houde 1972; Houde et al. 1974).

An example of duration-corrected abundance data at estimated mean ages for eggs and larvae up to 20.0 mm in 1973 is given in Table 8. In this example the mean daily growth increment was

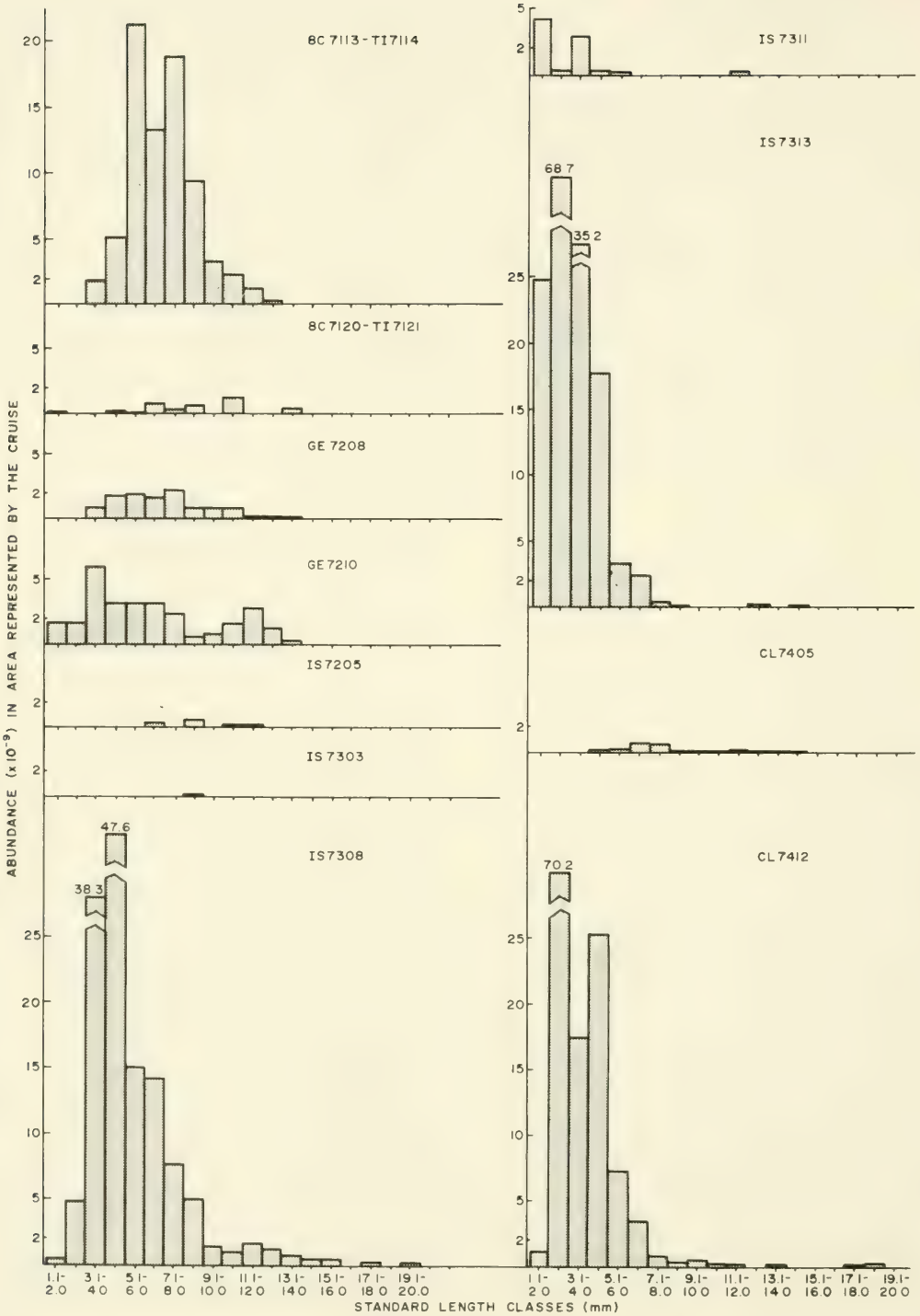

FIGURE 7.—Length–frequency distributions of scaled sardine larvae for 1971–74 cruises to the eastern Gulf of Mexico. Frequencies are expressed as estimated abundance of larvae in each length class within the area represented by the cruise. No adjustments for abundance have been made for cruises that did not cover the entire area where scaled sardine larvae might occur.

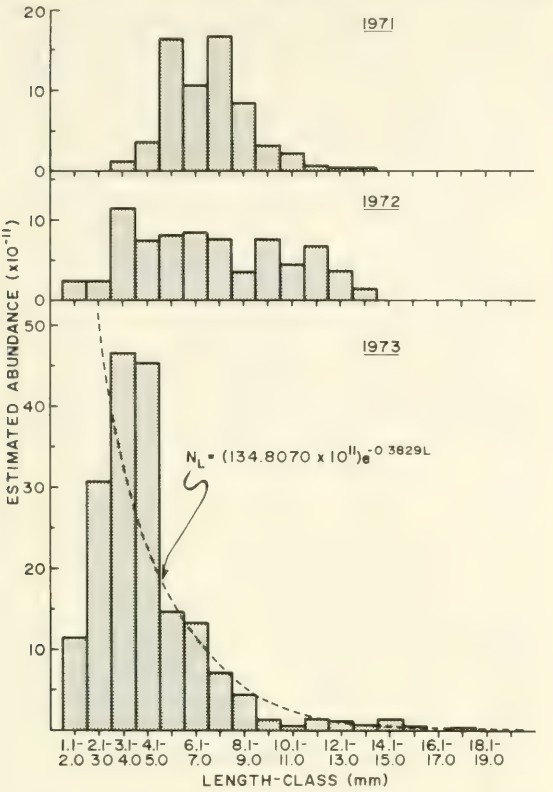

FIGURE 8.—Length–frequency distribution of annual larval abundance estimates for scaled sardine larvae collected in the eastern Gulf of Mexico, 1971–73. Frequencies in each 1-mm length class are expressed as estimated annual abundance and have been corrected for daytime avoidance. A fitted exponential function for 1973 data provides an estimate of the instantaneous coefficient of decline in abundance by length.

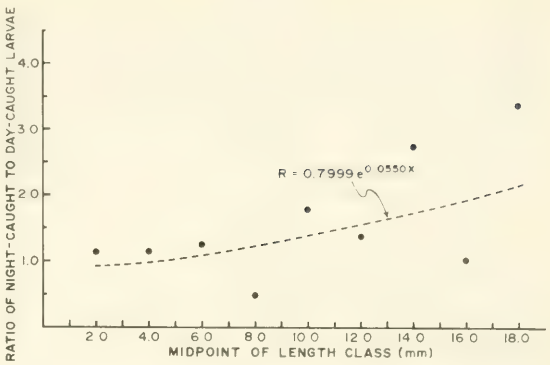

FIGURE 9.—Night to day ratios of sums of catches, standardized to numbers under 10 m² of sea surface, for scaled sardine larvae collected in 1971–74 in the eastern Gulf of Mexico. The ratios were calculated for larvae within each 2-mm length class from 1.1 to 19.0 mm SL. A fitted exponential regression describes the relationship. Larval abundance estimates for each length class at stations occupied during daylight were corrected by the appropriate ratio factor for each length class to account for daytime avoidance.

set at 0.8 mm and nonfully vulnerable larval stage duration was 1.0 day. I believe that those values are the best estimates for scaled sardine larvae, but other values also were assigned from which both mean ages and duration-corrected abundances were generated. Duration-corrected abundances (Table 8) were regressed on mean ages in an exponential regression to estimate the instantaneous mortality coefficient (Z) for age in days.

Mortality coefficients were calculated for various combinations of mean daily growth increments and durations of the nonfully vulnerable larval stage for 1973 data (Table 9). Possible values of the mortality coefficient, Z, range from 0.1822 to 0.3471, which correspond to daily percentage losses of 16.7 to 29.3%. For data from Table 8, where mean daily growth increment was 0.8 mm and nonfully vulnerable larval stage

TABLE 8.—An example of data from 1973 used to obtain stage duration, mean age, and duration-corrected abundance of scaled sardine eggs and larvae. Duration-corrected abundances were subsequently regressed on mean ages to obtain mortality rates (Table 9). Abundance estimates in the second column of the Table were previously corrected for daytime avoidance. In this example, the mean daily growth increment ($\bar{b}$) was set at 0.80. The nonfully vulnerable size classes were 1.1 to 3.0 mm. Calculating procedures were given in Houde (1977a), equations (12) to (16). The regression for these data is presented as Figure 10.

Stage	Abundance (no. × 10^{11})	Duration (days)	Mean age (days)	Duration-corrected abundance (no. × 10^{11})
Eggs	827.54	0.81	0.41	1,025.83
1.1– 3.0 mm	43.27	1.00	1.33	43.27
3.1– 4.0	46.63	2.89	3.21	16.14
4.1– 5.0	45.49	2.25	6.06	20.23
5.1– 6.0	14.71	1.84	8.33	7.99
6.1– 7.0	13.20	1.56	10.22	8.47
7.1– 8.0	7.25	1.35	11.84	5.36
8.1– 9.0	4.52	1.19	13.26	3.79
9.1–10.0	1.45	1.07	14.52	1.35
10.1–11.0	0.84	0.97	15.66	0.87
11.1–12.0	1.65	0.88	16.69	1.87
12.1–13.0	1.24	0.81	17.63	1.52
13.1–14.0	0.83	0.75	18.50	1.11
14.1–15.0	1.56	0.70	19.31	2.23
15.1–16.0	0.61	0.66	20.07	0.93
16.1–17.0	0.05	0.62	20.78	0.09
17.1–18.0	0.39	0.58	21.44	0.68
18.1–19.0	0.00	0.55	22.07	—
19.1–20.0	0.04	0.52	22.67	0.07

duration was 1.0 day, the estimated mortality coefficient is $Z = 0.2835$, corresponding to a 24.7% daily loss rate (Figure 10). The most probable scaled sardine mortality estimate for abundance at age data, $Z = 0.2835 \pm 0.0754$ at the 0.95 confidence level, is similar to those for thread

TABLE 9.—Summary of mortality estimates for scaled sardine larvae from the eastern Gulf of Mexico, 1973. Estimates were obtained from the exponential regression of egg and larvae abundances on mean age. Instantaneous growth and mortality coefficients were calculated for various possible combinations of mean daily growth increment and duration of the nonfully vulnerable larval stages. Egg stage duration was assigned the value 0.81 days. Nonfully vulnerable larval lengths were 1.1 to 3.0 mm SL. Explanation of the estimating method is given in equations (12) to (16) of Houde (1977a).

Mean daily growth increment, b (mm)	Instantaneous growth coefficient, g	Nonfully vulnerable larvae duration (days)	Instantaneous mortality coefficient, Z	Y-axis intercept, N_0 (no. $\times 10^{11}$)	Daily mortality rate, $1 - \exp(-Z)$
0.5	0.0552	1.0	0.1842	97.32	0.1683
0.6	0.0662	1.0	0.2179	116.45	0.1958
0.7	0.0772	1.0	0.2509	136.44	0.2220
0.8	0.0883	1.0	0.2835	157.36	0.2469
0.9	0.0993	1.0	0.3156	179.28	0.2706
1.0	0.1103	1.0	0.3471	202.26	0.2933
0.5	0.0552	3.0	0.1822	131.23	0.1665
0.6	0.0662	3.0	0.2146	164.36	0.1932
0.7	0.0772	3.0	0.2461	200.90	0.2182
0.8	0.0883	3.0	0.2767	240.98	0.2417
0.9	0.0993	3.0	0.3065	284.66	0.2640
1.0	0.1103	3.0	0.3353	332.06	0.2849

herring ($Z = 0.2124$ in 1971 and $Z = 0.2564$ in 1973), but higher than those for round herring: $Z = 0.1317$ in 1971–72 and $Z = 0.1286$ in 1972–73 (Houde 1977a, b).

The y-axis intercepts (N_0) of the regressions in Table 9 also estimate the number of eggs spawned in 1973. Their values are lower than those calculated by the Sette and Ahlstrom (1948) method for 1973 (Table 4), which is considered the best estimate of annual spawning. A higher than expected mortality rate of eggs or nonfully vulnerable larvae may have caused the discrepancy (Figure 10). Larval mortality, considering only fully vulnerable stages, may be lower than that for the entire egg–larval stage. For data from Table 8 and Figure 10, the mortality coefficient for fully vulnerable 3.1- to 20.0-mm larvae is $Z = 0.2458$, a daily loss rate of 21.8%.

The numbers of probable survivors at hatching, 5.5 mm, and 15.5 mm were estimated in 1973 for three instantaneous growth rates that likely encompass the true rate for scaled sardine larvae (Table 10). Initial egg abundance was the 1973 estimate from Table 4. The estimated number alive at each stage was calculated from the parameters of the exponential functions (Table 9) and from the estimated age in days at each stage (Table 8).

Mortality was high during the egg and larval stages. An apparent mortality of 85 to 91% occurred between spawning and hatching (Table 10). Less than 2% survived to 5.5 mm, when larvae would have been feeding for 2 days at 26° to 28°C (Houde et al. 1974). More than 99.9% mortality had occurred by 15.5 mm, when larvae were beginning to transform to juveniles. At the most probable growth rate, $g = 0.0883$, only 5 larvae/10,000 spawned eggs were estimated to have survived to 15.5 mm and 20 days of age in 1973.

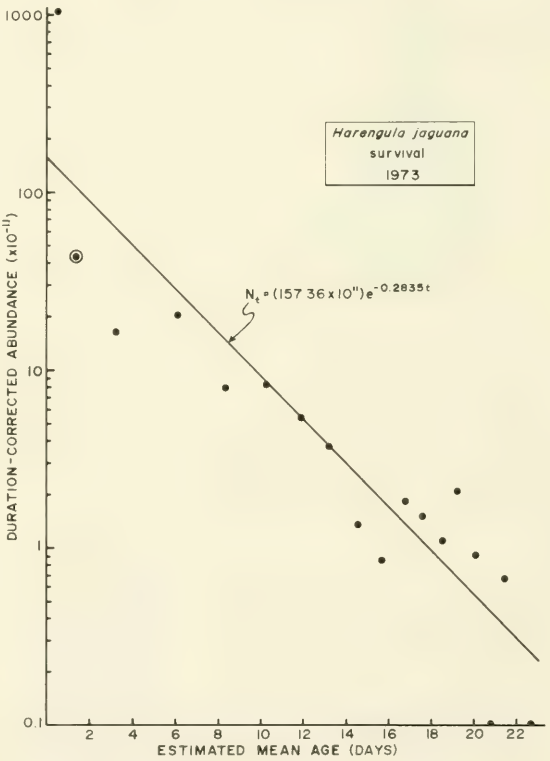

FIGURE 10.—Estimated abundance of egg and larval stages of scaled sardines in the eastern Gulf of Mexico in 1973. Abundance is expressed as a function of estimated age. A fitted exponential function gives an estimate of the instantaneous rate of decline in abundance for eggs and larvae up to 23 days of age. The symbol enclosed in the circle represents the nonfully vulnerable 1.1- to 3.0-mm length classes and was not included in the regression estimate of instantaneous decline.

TABLE 10.—Estimated numbers and percentages of survivors of scaled sardines at hatching, 5.5 mm SL, and 15.5 mm SL in 1973. Estimates are made at three possible growth rates (see Table 9). Duration of the nonfully vulnerable larval stage was set at 1.0 day for 1.1 to 3.0 mm larvae. The number of spawned eggs was based on the estimate in Table 4. Predicted numbers at hatching, 5.5 mm, and 15.5 mm are calculated from exponential functions based on Table 9 data.

Instantaneous growth coefficient, g	Number of spawned eggs ($\times 10^{11}$)	Instantaneous mortality coefficient, Z	Number hatching ($\times 10^{11}$)	Percent mortality[1] to hatching	Number of 5.5-mm larvae ($\times 10^{11}$)	Percent mortality to 5.5 mm	Number of 15.5-mm larvae ($\times 10^{11}$)	Percent mortality to 15.5 mm
0.0662	1,025.83	0.2179	97.61	90.5	11.82	98.8	0.39	99.96
0.0883	1,025.83	0.2835	125.07	87.8	14.83	98.6	0.53	99.95
0.1103	1,025.83	0.3471	152.69	85.1	17.63	98.3	0.68	99.93

[1]Hatching assumed to occur at 0.81 day.

Estimated survival of scaled sardines at hatching and 5.5 mm was lower than that for thread herring or round herring (Houde 1977a, b). In 1973 scaled sardines apparently experienced high mortality during embryonic and young larval stages, which quickly reduced the initial number of eggs to relatively few larvae. Thread herring and scaled sardine mortality rates may be similar for larvae in the fully vulnerable length classes. Round herring larvae had a lower estimated mortality rate than either scaled sardines or thread herring. But, the probable slower growth rate of round herring larvae at cooler temperatures (Houde 1977a) caused estimated numbers at 15.5 mm to be only 40 to 120 survivors/10,000 spawned eggs, which was comparable with the thread herring estimate of 60 to 200 survivors/10,000 eggs, but higher than the 5 survivors/10,000 eggs estimated for scaled sardines.

SUMMARY

1. Scaled sardines spawned from January to September in the eastern Gulf of Mexico, with most spawning occurring during spring and summer. They spawned in waters <30 m deep, mostly within 50 km of the coast.

2. Eggs were collected where surface temperatures ranged from 20.8° to 30.7°C and surface salinities were 29.9 to 36.9‰. Larvae ≤5.0 mm SL were collected at surface temperatures from 18.4° to 30.5°C and at surface salinities of 27.3 to 36.9‰. Most eggs and ≤5.0-mm larvae occurred where surface temperature exceeded 24°C and surface salinity was above 35‰.

3. Estimates of annual spawning increased in each year, 1971–73. Biomass estimates increased from 16,000 to 390,000 metric tons during those years. The mean biomass estimate for the 3-yr period was 184,527 metric tons. Concentrations of adult biomass between the coast and the 30-m depth contour were: 1971—2.8 kg/ha; 1972—24.7 kg/ha; 1973—64.8 kg/ha.

4. Estimated annual potential yields to a fishery were: 1971—4,177 to 8,354 metric tons; 1972—37,064 to 74,128 metric tons; 1973—97,153 to 194,305 metric tons. Potential yield, based on the 3-yr mean biomass estimate, was between 46,132 and 92,264 metric tons, or 7.7 to 15.4 kg/ha.

5. Larvae were more abundant in 1973 than in 1971 or 1972. Larval mortality, relative to length and to estimated ages, was estimated for 1973 data. For length, the instantaneous coefficient was $Z = 0.3829$, corresponding to a 31.8% decrease in larval abundance per millimeter increase in length. For age, the most probable estimate is $Z = 0.2835$, which corresponds to a 24.7% daily loss rate.

6. It is probable that more than 99.9% mortality occurred between spawning and the 15.5-mm stage in 1973. Only 5 larvae/10,000 spawned eggs were estimated to have survived to 15.5 mm at 20 days of age in that year.

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NOTES

REPRODUCTIVE PARAMETERS OF THE OFFSHORE SPOTTED DOLPHIN, A GEOGRAPHICAL FORM OF *STENELLA ATTENUATA*, IN THE EASTERN TROPICAL PACIFIC, 1973–75

Perrin et al. (1976) presented estimates of reproductive parameters of the offshore population of *Stenella attenuata* in the eastern Pacific based on data collected in 1968–73, inclusive. The sample included 3,527 specimens. Only the 1973 sample (2,036) was putatively cross-sectional with respect to age and sex structures of the kill; in earlier years, adult females were selected for examination. The purpose of this paper is to present analyses of samples collected in uniform fashion in 1973, 1974, and 1975, updating the prior report and providing a uniformly developed, albeit short, time series of annual estimates.

Methods and Materials

The data and specimens were collected by NMFS biological technicians aboard commercial tuna vessels. Data collection procedures were the same as described by Perrin et al. (1976). Data on *S. attenuata* were collected on 24 cruises in 1973, 33 in 1974, and 32 in 1975.

The total sample includes 6,243 specimens, 6,168 from precisely known localities (Figure 1). Because of the seasonal nature of the fishery, the sample is heavily biased toward the first half of the calendar year with practically no coverage of the summer months (Table 1).

Laboratory procedures were the same as reported by Perrin et al. (1976), but the analytical methods differed slightly. In calculating gross annual reproductive rate (proportion female × proportion of total females which are reproductive

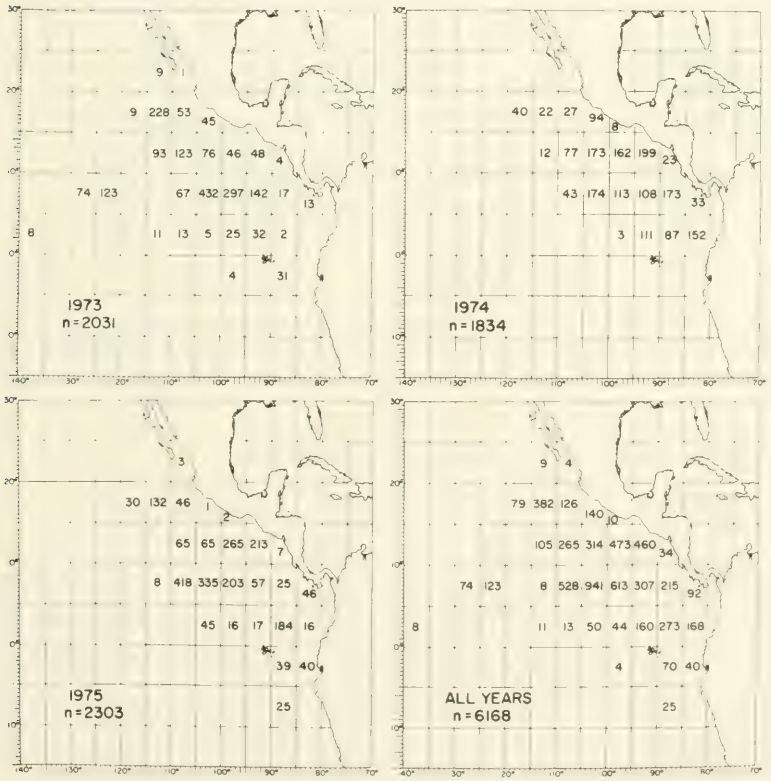

FIGURE 1.—Sample of the offshore spotted dolphin, *Stenella attenuata*, collected in 1973–75, by 5° squares.

TABLE 1.—The sample of the offshore spotted dolphin, *Stenella attenuata*, by sex, year, and month, 1973–75. Date of capture was not available for 18 of the total 6,243 specimens collected.

Month	1973		1974		1975		Total	
	♂	♀	♂	♀	♂	♀	♂	♀
Jan.	267	326	239	300	395	442	901	1,068
Feb.	200	231	428	532	249	312	877	1,075
Mar.	137	210	66	72	133	153	336	435
Apr.	41	46	35	42	135	183	211	271
May	85	156	5	2	34	35	124	193
June	56	69	36	9	30	47	122	125
July	0	0	0	0	6	12	6	12
Aug.	0	0	11	13	2	4	13	17
Sept	0	0	1	4	0	0	1	4
Oct.	5	16	0	0	31	51	36	67
Nov	72	103	20	48	32	39	124	190
Dec.	8	9	0	0	0	0	8	9
Totals	871	1,166	841	1,022	1,047	1,278	2,759	3,466
	2,037		1,863		2,325		6,225	

× annual pregnancy rate), Perrin et al. (1976) estimated the proportion of adult females which were reproductive from coloration phase data, based on a subsample of data on percentage mature in the various coloration phases ("mottled" and "fused–adult"). In the present study, a much larger sample of complete reproductive data was available; therefore, the proportion of total females which were reproductive was estimated directly from that sample. Specimens for which ovarian data were lacking or incomplete were allocated to mature or immature categories based on a length criterion. Average length at attainment of sexual maturity was estimated as that length (177 cm) at which the number of shorter but mature specimens in the sample equals the number of longer but immature specimens.

Results and Discussion

Calving Cycle and Pregnancy Rate

The calving cycle, for purposes of analyzing field data, can be divided into three phases: 1) pregnancy, 2) lactation, and 3) "resting" (a catch-all phase for animals neither pregnant nor lactating, which includes females truly resting, i.e., not ovulating because of being between cycles, those which have just ovulated but have not become pregnant, some with extremely small embryos missed in dissection, those which recently aborted, and those which have prematurely terminated lactation due to death of the suckling calf).

We estimated the length of the cycle (and pregnancy rate) in two ways: 1) based on the reproductive structure of the sample of adult females, i.e., based on the assumption that the samples are not biased with respect to reproductive phase, and that the proportion of a sample of mature females in a particular phase is directly proportional to the relative length of that phase, using the previously estimated (Perrin et al. 1976) length of gestation (11.5 mo) as a time calibration, and 2) based on the estimate of length of gestation and a largely independent estimate of length of lactation.

The first estimate was based on data for 1,876 females classified as pregnant, lactating, pregnant and lactating, "resting," or postreproductive (Table 2). The "resting" females were further subdivided into those with and without a corpus luteum. As discussed above, some proportion of those with a corpus luteum can be assumed to represent females not truly resting (with a corpus luteum of infertile ovulation). In the total sample of 3,443 females, 61 were simultaneously pregnant and lactating (6.1% of the lactating females). Minor differences between the numbers in Table 2 and in table 8 of Perrin et al. (1976) reflect increase of the 1973 sample by eight specimens and reexamination and reevaluation of the materials.

Subtraction of the postreproductive females from the aggregate of mature females of determined reproductive condition and allocation of the females both pregnant and lactating to both

TABLE 2.—Reproductive condition of 3,469 female offshore spotted dolphins, *Stenella attenuata*, collected 1973–75.

Condition	1973		1974		1975		1973–75 pooled	
	No.	%	No.	%	No.	%	No.	%
Sexually immature	522	45.0	465	45.9	580	45.7	1,567	45.5
Sexually mature:								
Condition undetermined	58	5.0	60	5.9	191	15.0	309	9.0
Pregnant only	232	20.0	122	12.1	119	9.4	473	13.7
Pregnant and lactating	16	1.4	23	2.3	22	1.7	61	1.8
Lactating only	226	19.5	256	25.3	264	20.8	746	21.7
"Resting"								
With corpus luteum	34	2.9	32	3.2	28	2.2	94	2.7
Without corpus luteum	66	5.7	48	4.7	64	5.0	178	5.2
Postreproductive	7	0.6	6	0.6	2	0.2	15	0.4
Totals	1,161	100.0	1,012	100.0	1,270	100.0	3,443	100.0

categories provides estimates of the proportions of reproductive females in the three phases of the cycle and, comparing the proportions, of the relative lengths of the phases. Estimated average length of the phases and the total cycle can then be calculated for each 1-yr sample and for the pooled samples, based on the relative lengths of the phases and on the estimated gestation period of 11.5 mo (Method 1 in Table 3). The estimates of average length of cycle thus derived trend from 27.3 mo in 1973 to 42.3 mo in 1975, due to increase in the estimated length of lactation from 11.2 mo to 23.3 mo.

Annual pregnancy rate under Method 1 (also in Table 3) is calculated as proportion of reproductive females pregnant divided by the length of gestation (0.958 yr). The reciprocal of annual pregnancy rate is the estimate of average calving interval.

In the second method of calculating length of calving cycle, we estimated length of lactation by assuming that a suckling calf existed in the samples for each lactating female. Under this assumption, the length at which the cumulative frequency of calves in a sample equals the number of lactating females should be the average length at weaning (from which, using the length–age equations published by Perrin et al. (1976), the average age at weaning can be calculated). If the length of lactation increases, the average length at weaning estimated by this method should increase concomitantly. The calculated length at weaning did not increase sharply between years (Table 4). Under Hypothesis II of Perrin et al. (1976) of the rate of deposition of dentinal growth layers (two in first year and one per year thereafter—the most likely alternative), the estimated length of lactation ranges from 11.2 mo in 1973 to 12.4 mo in 1974. To arrive at estimates of the total length of the calving cycle under Method 2, we used the estimate of time spent in the "resting" phase under Method 1 for 1973 (the year for which the two estimates of length of lactation coincide exactly) or 4.6 mo, for each of the three annual estimates. This estimate is based on the assumptions under Method 1 but must suffice as a first approximation. In estimating pregnancy rate (as reciprocal of calving interval)—Table 3—overlapping cycles were taken into consideration by adjusting the effective length of lactation downward by a factor equal to the percentage of lactating females also pregnant.

The 1973 estimate of length of lactation (and length of cycle, pregnancy rate, and calving interval) is very close to that obtained by Method 1 above (11.2 mo), but the two sets of estimates diverge sharply thereafter. The first method could be invalid and cause diverging estimates if 1) lactating females (and their nursing calves) were overrepresented in the samples for 1974 and 1975 or, conversely, 2) either (or both) pregnant or "resting" females were underrepresented. The first situation could obtain if lactating females and their accompanying calves are more likely to be captured and killed in the net because of limited endurance and ability to escape of the calf, certainly less than those of adults, and the strength of the mother–calf bond. The second method could yield erroneous estimates if 1) nursing calves were overrepresented in the samples or,

TABLE 3.—Estimates of lengths of reproductive phases, pregnancy rate, and calving interval under two methods of estimating length of calving cycle (see text) of the offshore spotted dolphin, *Stenella attenuata*, 1973–75.

Item	1973	1974	1975	1973–75 pooled
Sample size (no.)	574	481	497	1,552
Pregnancy (mo)	11.5	11.5	11.5	11.5
Lactation (mo):				
Method 1	11.2	21.9	23.3	17.4
Method 2 (Hyp. II)	11.2	12.4	12.1	11.9
"Resting" (Method 1)	4.6	6.4	7.5	5.9
Sum of phases:				
Method 1				
Months	27.3	39.8	42.3	34.8
Years	2.28	3.32	3.53	2.90
Method 2				
Months	27.3	28.5	28.2	28.0
Years	2.28	2.38	2.35	2.33
Annual pregnancy rate (APR):				
Method 1	0.452	0.314	0.296	0.359
Method 2	0.472	0.459	0.461	0.463
Calving interval (1/APR):				
Method 1				
Years	2.21	3.18	3.38	2.79
Months	26.5	38.2	40.5	33.4
Method 2				
Years	2.12	2.18	2.17	2.16
Months	25.4	26.2	26.0	25.9

TABLE 4.—Estimates of length of lactation in the offshore spotted dolphin, *Stenella attenuata*, based on the cumulative calf length/lactating females method (see text) 1973–75.

Sample	Lactating females[1] (no.)	Length[2] (cm)	Length of lactation			
			Growth layers	Under hypothesis I (mo)	II (mo)	III (mo)
1973	259	135.8	1.86	11.2	11.2	11.2
1974	301	138.5	2.03	12.2	12.4	12.2
1975	376	138.2	2.01	12.1	12.1	12.1
1973–75 pooled	936	137.8	1.98	11.9	11.9	11.9

[1]Includes mature females (≥177 cm) without lactation data prorated to lactating and nonlactating based on proportions in sample with lactation data.
[2]Length at which cumulative number of calves = number of lactating females.

conversely, 2) lactating females were underrepresented. Ongoing analyses of data for the spotted dolphin, *S. attenuata* (J. E. Powers pers. commun.), indicate that small calves are probably overrepresented in small single-set samples. In addition, the absence of sharp change in length of calves at weaning as estimated by the cumulative-calves method speaks against the alternative explanation of development between the years of differential bias against calves and lactating females. The balance of evidence favors the first alternative above, that of progressive overrepresentation of both nursing calves and lactating females as the average number of animals encircled has increased and the average number killed per net haul has decreased[1] accentuating the factor of differential stamina.

Gross Annual Reproduction

Estimates of gross annual reproductive rates can be calculated based on the two methods of estimating pregnancy rate (Table 5). It must be noted that if, as discussed above, small calves are overrepresented in small samples (which make up most of the aggregate sample), then pregnancy rate (and, therefore, gross annual reproductive rate) under Method 1 are underestimated to an unknown, but probably small, degree. This factor, of course, would also cause overestimation of the proportion of the total sample female and the proportion of total females which are reproductive, causing a countering overestimation of gross annual reproduction of unknown, but again probably small, size.

Standard errors are attached to the various estimates where sample size ≥ 100, under the assumption that the binomial distribution tends to normality in large samples (Bailey 1959), allowing calculation of the standard error as:

$$SE = \sqrt{p(1-p)/n}$$

where p = proportion (estimate of parameter)
n = sample size.

Although gross annual reproductive rate as calculated in Table 5 is a product of three estimates, it can be calculated directly from the total sample (number of females pregnant ÷ total number of males and females), to yield the same estimate and allowing estimation of the variance by the above method. The total sample size was adjusted downward by a factor equal to the proportion of mature females in unknown reproductive condition. The effect on the variance by the constant used to adjust the pregnancy rate to an annual rate was ignored, because the constant (11.5 mo gestation ÷ 12 mo, or 0.958) is close to unity.

The estimates of pregnancy rate (and gross annual reproductive rate) for 1973 and 1974 based on structure of the samples (Method 1) are significantly different from each other (using ±2 SE as an approximation of a 95% confidence interval), and the estimate for 1975, although not statistically different from that for 1974, continues the trend. The estimates based on independent esti-

[1]Staff, Porpoise/Tuna Interaction Program, Oceanic Fisheries Resources Division. 1975. Progress of research on porpoise mortality incidental to tuna purse-seine fishing for fiscal year 1975. SWFC Admin. Rep., Natl. Mar. Fish. Serv., La Jolla, Calif., LJ-75-68, 98 p. (Unpubl. rep.)

TABLE 5.—Calculation of estimates of gross annual reproductive rate of offshore spotted dolphin, *Stenella attenuata*, for 1973–75, using two alternative estimates of pregnancy rate (see text). Standard error follows estimate (see text).

	A	B	C		A × B × C	
			Annual pregnancy rate		Gross annual reproductive rate	
Year	Proportion female	Proportion of females reproductive	Method 1	Method 2	Method 1	Method 2
1971			0.546 (86)			
1972			0.465 ± 0.023 (455)			
1973	0.572 ± 0.011 (2,037)	0.544 ± 0.015 (1,161)	0.452 ± 0.021 (574)	0.472 ± 0.021 (574)	0.141 ± 0.008 (2,036)	0.147 ± 0.008 (1,934)
1974	0.548 ± 0.012 (1,863)	0.535 ± 0.016 (1,012)	0.314 ± 0.021 (481)	0.459 ± 0.023 (481)	0.092 ± 0.007 (1,860)	0.135 ± 0.008 (1,750)
1975	0.559 ± 0.010 (2,321)	0.542 ± 0.014 (1,270)	0.296 ± 0.020 (523)	0.461 ± 0.022 (523)	0.087 ± 0.006 (2,321)	0.140 ± 0.007 (2,001)
1973–75	0.560 ± 0.006 (6,221)	0.541 ± 0.008 (3,443)	0.359 ± 0.012 (1,578)	0.463 ± 0.012 (1,578)	0.109 ± 0.004 (6,243)	0.140 ± 0.004 (5,685)

mates of lengths of gestation and lactation also trend downward, but the year-to-year differences are not statistically significant. As discussed above, the balance of evidence favors the (relatively nonvarying) estimates based on Method 2.

Although adequate data for estimating sex ratio and proportion of total females which were reproductive in 1971 and 1972, using the methods employed here, or for estimating pregnancy rate using Method 2, are not available because of selection of adult females for dissection, the estimates of pregnancy rate (using Method 1) for those two years are included in Table 5. The sample for 1971 is too small to allow direct statistical comparison with the estimates for later years, but the 1972 estimate is not significantly different from the estimates for 1973, reinforcing the suggestion that a major shift in population structure or (more likely) in degree of representativeness of the kill or the sample occurred in 1974.

In summary, the balance of evidence indicates that, in management of the dolphin/tuna situation, changes in the structure of the dolphin kill, per se, should not be taken to necessarily mean that parallel changes in reproductive rates have occurred. The changes more likely represent sampling artifacts caused by changes in the fishing and dolphin rescue operations.

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THE UPTAKE, DISTRIBUTION, AND DEPURATION OF ^{14}C BENZENE AND ^{14}C TOLUENE IN PACIFIC HERRING, *CLUPEA HARENGUS PALLASI*

This note is a sequel to Korn et al. (1976), where uptake, distribution, and depuration of ^{14}C benzene were examined in striped bass, *Morone saxatilis*, and northern anchovy, *Engraulis mordax*. Like benzene, toluene is a prevalent, water-soluble, and toxic monoaromatic component of petroleum and associated products. According to Anderson et al. (1974a), toluene is second only to benzene as the most abundant aromatic oil component in the water-soluble extracts of southern Louisiana and Kuwait crude oils (6.75–3.36 μl/liter benzine; 4.13–3.62 μl/liter toluene, respectively).

Although levels of the volatile aromatics are thought to be low in areas subject to chronic oil exposure, few actual measurements have been made. Further, if fish can accumulate benzene and if energy is required to metabolize, detoxify, and depurate these aromatics, long-term physiological and population effects are possible.

In this study, a comparison of the uptake, distribution, and depuration of ^{14}C benzene and ^{14}C toluene, at a low sublethal concentration [100 parts per billion (ppb)], was undertaken to determine which of these prevalent aromatics may pose the greatest problem. It was hypothesized that, although toluene is less soluble in seawater (Anderson et al. 1974a), it may be more toxic and exhibit greater accumulation levels and persistence. Our previous work with striped bass and northern anchovy indicated other tissues that should be examined, such as kidney, pyloric caeca, gonad, and intestine, and in the present comparison, residues in the additional tissues were measured. Pacific herring, *Clupea harengus pallasi*, were selected as test animals because of their importance as estuarine and nearshore forage fish for many important recreational and commercial species, including striped bass and chinook salmon.

Methods

Pacific herring were obtained from a San Francisco Bay bait dealer and were transported directly to the Tiburon Laboratory dock. The fish were acclimated under test conditions for at least 2

wk in 2,000-liter tanks. Fish were not in spawning condition.

In each of two separate studies, 10 fish were placed into each of six 660-liter fiber glass tanks and further acclimated for 1 wk before exposure. Salinity and temperature were 24‰ and 9°–11°C, respectively, during the acclimation and test periods. In the first study, fish were exposed to 100 nl/liter (ppb) ^{14}C benzene (4.2 dpm/ng specific activity). In the second study, fish were exposed to 100 nl/liter (ppb) ^{14}C toluene (3.2 dpm/ng specific activity). In both studies, one of the six tanks was a control, with no exposure. Exposures were static (single dose with delining concentration) for 48 h, preceded and followed by a continuous water flow of 2 liters/min.

Water samples for radiometric aromatic analyses were taken from all tanks at 0, 6, 24, and 48 h after initial dosage. Gallbladder, intestine, pyloric caeca, gill, brain, liver, muscle, kidney, and immature male and female gonad tissues were sampled for radiometric analyses at 6 h, then daily for 7 days.

Methods of exposure and radiometric analyses are identical to Korn et al. (1976), except that the tissues from fish exposed to toluene were digested at 50°C for 24 h.

Since accumulation levels in the gallbladder were based solely on radiometric analysis of the ^{14}C present and could include metabolites of the monoaromatics as well as unchanged benzene or toluene, an additional study was made to interpret the residue. Two groups of fish, with six fish per tank, were exposed to 100 nl/liter ^{14}C benzene (1 tank), and 100 nl/liter ^{14}C toluene (1 tank) for 48 h. Exposure was the same as in the above experiments. At the end of the 2-day exposure, the gall bladders were removed, weighed, and extracted with 0.2 ml trifluorotrichloroethane-Freon.[1] The extracts were analyzed for benzene and toluene by gas chromatography (Benville and Korn 1974). Efficiency of extraction was not determined and therefore the gas chromatography analyses were more qualitative than quantitative.

Results and Discussion

There were no mortalities in either exposed or control fish. Unlike herring exposed during spawning condition (Struhsaker 1977), no abnormal behavior was noted, thus immature herring appear less sensitive to exposures than mature herring in spawning condition.

The concentration of benzene and toluene in seawater in all tanks declined linearly ($\hat{Y} = a + bX$ where $\hat{Y}$ = concentration in microliters per liter, a = initial concentration in microliters per liter, b = rate of decline in microliter per liter per hour, and X = time in hours), during the 48-h static exposure, as follows:

Item	*Benzene*	*Toluene*
Total no. samples	20	20
a ($\hat{Y}$-intercept)	0.094997	0.09195
b	−0.0006075	−0.0007587
Percentage of initial concentration remaining:		
24 h	85	80
48 h	69	60

The equation for decline in benzene and toluene is probably a function of the volume of seawater. In earlier studies, at smaller volumes, decline was exponential over the 48-h static exposure. At the volume in these experiments it was linear, but probably would have been exponential over a longer time period. The rate of decline appears to decrease with increasing volume.

In all herring tissues, toluene accumulated to higher levels than did benzene (Table 1), despite the faster loss of toluene compared with benzene from the test solution. Certain trends were common to both aromatic components. The tissue exhibiting the highest accumulation was the gallbladder (3.1 nl/g benzene, 34 nl/g toluene, maximum level). The lowest level of maximum accumulation was found in the immature gonad (0.24 nl/g benzene, 0.44 nl/g toluene). Pyloric caeca and intestine contained varying amounts of bile and therefore had a wide range of ^{14}C activity and a resulting wide variance in calculated concentrations.

Benzene was accumulated up to 31 times the initial water concentration (gallbladder) and toluene reached 340 times the initial water concentration (gallbladder).

In most tissues, and for most components, maximum accumulation levels were reached rapidly. Within 24 h, maximum residues were obtained in all tissues except the gallbladder and pyloric caeca. Toluene accumulated to the maximum level (0.25 days) before benzene peaked (1–2 days) in all tissues except the gallbladder and intestine.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Residues of benzene and toluene and/or metabolites (mean nl/g±SE) accumulated during and after a 48-h exposure to 100 nl/liter (ppb) ^{14}C benzene or 100 nl/liter (ppb) ^{14}C toluene in the tissues of *Clupea harengus pallasi*. Number of samples in parentheses.

Tissue and compound	Time (days) from start of exposure[1]							
	Uptake			Depuration				
	0.25 (6 h)	1	2	3	4	5	6	7
Gallbladder:								
Benzene	0.37±0.075 (4)	2.1±0.71 (5)	3.1±0.48 (5)	2.7±1.5 (3)	0.56±0.30 (3)	0.92±0.79 (4)	0.60±0.14 (4)	0.61 (1)
Toluene	4.6±3.4 (5)	30±11 (5)	27±15 (5)	34±17 (5)	19±9.0 (5)	1.7±0.95 (5)	0.24±0.49 (3)	6.0±4.9 (2)
Intestine:								
Benzene	0.83±0.78 (4)	0.42±0.28 (5)	0.61±0.55 (5)	0.16 (1)	—[2] —	0.087 (1)	0.081 (1)	— —
Toluene	3.9±2.4 (5)	2.3±2.1 (4)	2.1±1.7 (5)	0.70±0.7 (5)	0.09±0.014 (2)	0.092±0.013 (3)	0.11±0.025 (2)	0.13±0.70 (3)
Pyloric caeca:								
Benzene	0.058±0.34 (5)	0.63±0.38 (5)	0.64±0.38 (5)	0.095±0.039 (3)	— —	0.056 (1)	— —	— —
Toluene	3.6±3.6 (5)	1.8±0.32 (5)	2.4±1.4 (5)	0.77±0.46 (5)	0.23±0.94 (5)	0.13±0.03 (5)	0.11±0.037 (5)	0.16±0.081 (4)
Gill:								
Benzene	0.51±0.12 (5)	0.61±0.33 (5)	0.73±0.46 (5)	0.073 (2)	0.068 (1)	— —	— —	— —
Toluene	1.8±0.58 (5)	1.2±1.2 (5)	1.0±0.96 (5)	0.20±0.12 (5)	— —	— —	— —	— —
Brain:								
Benzene	0.74±0.11 (5)	0.75±0.14 (5)	0.62±0.052 (5)	0.59 (2)	— —	— —	— —	— —
Toluene	2.1±0.19 (5)	2.0±0.28 (5)	1.5±0.18 (5)	0.13±0.073 (3)	— —	— —	— —	— —
Liver:								
Benzene	0.45±0.070 (5)	0.53±0.096 (5)	0.50±0.067 (4)	— —	— —	— —	— —	— —
Toluene	1.5±0.44 (5)	1.4±0.44 (5)	1.2±0.13 (5)	0.36±0.15 (5)	0.23±0 05 (4)	— —	— —	— —
Muscle:								
Benzene	0.41±0.22 (5)	0.63±0.36 (5)	0.44±0.33 (4)	0.035 (1)	0.066 (1)	— —	— —	— —
Toluene	1.3±0.80 (5)	0.52±0.28 (5)	0.66±0.71 (5)	0.33 (2)	— —	— —	— —	— —
Kidney:								
Benzene	0.32±0.066 (5)	0.32±0.066 (5)	0.40±0.12 (5)	— —	— —	— —	— —	— —
Toluene	1.3±0.50 (5)	1.1±0.40 (5)	0.75±0.33 (5)	0.18±0.099 (4)	— —	— —	— —	— —
Gonad:								
Benzene	0.15±0.021 (5)	0.24±0.062 (5)	0.21±0.10 (5)	— —	— —	— —	— —	— —
Toluene	0.43±0.24 (5)	0.44±0.21 (5)	0.44±0.28 (4)	0.16 (1)	— —	— —	— —	— —

[1]Exposure terminated after 2 days; then fish remained in flowing seawater for 5 days.
[2]— = nondetectable levels.

Residues were depurated rapidly, with most tissues having nondetectable amounts after 3–4 days (1–2 days after termination of exposure). The gallbladder, intestine, and pyloric caeca retained residues through the duration of the study (7 days).

In the experiment in which gas chromatographic analyses were performed on the gallbladder, no detectable benzene (<0.1 nl/g) was measured. Gas chromatography analysis resulted in only 0.56–1.5 nl/g toluene. This indicates that most or all of the radioactivity measured by liquid scintillation in the gallbladders of fish exposed to benzene is not the parent compound, but one or more metabolites. Fish exposed to toluene had a small amount of the parent compound as opposed to metabolites (1.5 nl/g toluene maximum, compared with 27 nl/g expected [Table 1]).

The above result and the occurrence of delayed depuration in the gallbladder, intestine, and pyloric caeca supports the contention that benzene and toluene are metabolized in the liver, stored in the gallbladder, then passed into the intestine and are excreted with the feces. This agrees with Roubal et al. (in press) who found high levels of benzene metabolites in the liver and gallbladder of salmon which had previously received intraperitoneal benzene injections. This also agrees with our previous results with benzene in other fishes (Korn et al. 1976), results of Neff (1975), and with work by Lee et al. (1972) who demonstrated metabolism of polycyclic aromatics in the liver

and subsequent storage in the gallbladder. Studies with polycyclic aromatics (naphthalene, benzpyrene) by other investigators (Lee et al. 1972; Anderson et al. 1974b; Neff 1975; Roubal et al. in press) indicate higher accumulation levels and slower depuration than we have found with benzene and toluene. However, different species are involved, and these higher aromatics are also less prevalent in the water-soluble extract of crude oil.

The results of this study are generally consistent with our previous work exposing striped bass and northern anchovy to ^{14}C benzene at the same initial concentration and exposure period (100 nl/liter for 48 h; Korn et al. 1976), except for the considerably higher accumulation in the anchovy than in the other species. This is probably primarily a result of the higher stress, activity level, and scale and mucus loss in anchovy while in captivity.

The gonads sampled in this study were immature and showed low accumulation levels. In another study exposing mature spawning herring to 100 nl/liter benzene for 48 h (Struhsaker 1977), higher accumulation occurred in the ovary, with associated deleterious effects on the ripe ovarian eggs and on development of larvae subsequent to exposure of the parental females.

Of the two components studied here, toluene would appear to be potentially a greater problem to fish. Toluene could be rapidly accumulated to high levels in fish after even a brief contact during an oil spill. Since toluene is one of the more prevalent water-soluble oil components, further research on the effects and uptake of this component are indicated. Further, chronic exposures are probably of more importance to the survival of fish populations than are spills, and studies of long-term exposure to chronic concentrations should be made.

Finally, the probability that benzene and toluene are rapidly metabolized or converted to metabolites (possibly phenol, which is also highly toxic) leads to the need for metabolite research. Uptake studies with phenolic metabolites would be of interest, as would be the determination of uptake over extended time intervals.

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FOOD HABITS AND FEEDING CHRONOLOGY OF RAINBOW SMELT, *OSMERUS MORDAX*, IN LAKE MICHIGAN[1]

Rainbow smelt, *Osmerus mordax* Mitchill, in Lake Michigan originated from a planting in Crystal Lake, Mich., in 1912 (Van Oosten 1937). Since its introduction in Lake Michigan, the smelt has become abundant, serving as forage for larger, predatory species (Wright 1968; Harney and Norden 1972) and sustaining a small seasonal sport and commercial fishery. There has been considerable controversy regarding the smelt's role as a piscivore. Food studies of smelt in Saginaw Bay, Lake Huron (Gordon 1961) and Lake Erie (Price 1963) have shown that smelt consumes fishes, but not the alewife, *Alosa pseudoharengus*. Recently, a fall collection of smelt revealed that it consumes young-of-the-year alewives (O'Gorman 1974).

The food habits of Lake Michigan smelt have not been studied on a seasonal basis and little information exists concerning its food habits during the winter months. Also, feeding chronology has never been considered. The purpose of this study was to examine food habits of smelt during 6 mo representing all four seasons and to consider feeding chronology during two representative months.

Materials and Methods

Rainbow smelt were collected along the western shore of Lake Michigan by gillnetting or trawling on six dates between March 1973 and June 1974 (Table 1). Gill nets were placed on the bottom overnight and 45-min trawl hauls performed at 4-h intervals over a 24-h period. Gill nets were set and retrieved at 4- to 6-h intervals over a 24-h period on 13 October 1973 in order to examine feeding chronology. Smelt were collected at different depths during the course of the study because of their seasonal inshore–offshore movements. Fish were frozen shortly after capture.

Feeding chronology was examined on 23 March and 13 October 1973. Stomachs of smelt used in this portion of the study were dissected out and the contents removed. Fish and stomach contents were dried for 48 h at 60°C and weighed to the nearest milligram. Dried stomach contents were expressed as a percentage of dry body weight. The significance of time of day on the amount of food in stomachs was ascertained with analysis of variance (ANOVA). Means and the ANOVA were calculated from arcsine transformed data (Sokal and Rohlf 1969). A chi-square contingency test was used to ascertain the significance of time of day on the occurrence of empty stomachs. Significance testing was performed at the 0.05 error level.

TABLE 1.—Dates, locations, depths, and methods of capture of Lake Michigan smelt examined in this study.

Collection date	Location (off shore from)	Depth (m)	Method of capture[1]
20 Feb. 1974	Algoma, Wis	85	Gill net
23 Mar. 1973	Two Rivers, Wis.	74	Bottom trawl[2]
21 May 1974	Milwaukee, Wis	18	Gill net
18 June 1974	Milwaukee, Wis	18	Gill net
15 Aug. 1974	Milwaukee, Wis	27	Gill net
13 Oct. 1973	Port Washington, Wis.	37	Gill net[2]

[1]All collections made on the bottom
[2]Feeding chronology examined

Separate smelt were examined for food habits. These fish were measured to the nearest millimeter in length. Stomachs were removed, contents of each stomach were placed in a Petri dish with water, and the organisms enumerated. Food habits were defined in terms of percentage numbers and percent dry weight of stomach contents (Wells and Beeton 1963). Dry weight indices used were fish, 176; *Mysis*, 3; *Pontoporeia*, 1; fingernail clam, 1; Tendipedidae, 0.4; and Cladocera-Copepoda, 0.003 (Morsell and Norden 1968).

Results

Stomachs of 515 smelt were examined. Food of smelt included *Mysis; Pontoporeia;* alewives (young-of-the-year and yearlings); and to a lesser extent, fingernail clams; Tendipedidae pupae; cladocerans; and copepods (Table 2, 3). A marked increase in piscivorous food habits was observed in smelt longer than 180 mm. For this reason, smelt were divided into two size groups.

Smelt shorter than 180 mm consumed primarily *Mysis* during October, February, and March (Table 2). Smelt were found in shallower water during May, June, and August and their stomachs contained yearling alewives, *Pontoporeia,* and Tendipedidae. *Pontoporeia* were consumed most frequently during August, when they represented 35% dry weight of the diet. Tendipeds represented 25, 6, and 2 percentage numbers of the diet during May, June, and August, respectively. However,

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TABLE 2.—Food habits of Lake Michigan smelt shorter than 180 mm total length. Upper values for food organisms represent dry weight and values in parentheses are the percentage numbers.

Collection date	Average and range of lengths (mm)	No. of stomachs examined	% of stomachs empty	Food organisms					
				Mysis	*Pontoporeia*	Alewife	Fingernail clam	Tendipedidae	Copepoda and Cladocera
20 Feb. 1974	147	79	42	98	1	—	1	—	—
	90–179			(95)	(3)		(2)		
23 Mar. 1973	138	80	36	100	—	—	—	—	—
	94–179			(100)					
21 May 1974	162	68	60	62	<1	37	<1	1	—
	109–179			(73)	(1)	(1)	(1)	(25)	
18 June 1974	160	62	61	42	—	58	—	<1	<1
	140–179			(12)		(1)		(6)	(82)
15 Aug. 1973	157	40	1	30	35	30	5	<1	1
	120–175			(26)	(61)	(1)	(9)	(2)	(2)
13 Oct. 1973	158	88	34	87	3	10	<1	—	—
	115–179			(88)	(9)	(1)	(2)		
Total	154	417	41	70	7	23	1	<1	<1
				(66)	(12)	(<1)	(2)	(6)	(14)

TABLE 3.—Food habits of Lake Michigan smelt 180 mm total length and longer. Upper values for food organisms represent percent dry weight and values in parentheses are the percentage numbers.

Collection date	Average and range of lengths (mm)	No. of stomachs examined	% of stomachs empty	Food organisms			
				Mysis	*Pontoporeia*	Alewife	Fingernail clam
20 Feb. 1974	210	21	43	39	1	60	—
	180–251			(93)	(5)	(2)	
23 Mar. 1973	206	20	25	95	5	—	—
	180–246			(86)	(14)		
21 May 1974	199	27	37	6	—	94	—
	181–238			(78)		(22)	
18 June 1974	206	10	60	1	—	99	—
	196–232			(33)		(66)	
15 Aug. 1973	201	8	12	93	6	—	1
	182–225			(82)	(16)		(1)
13 Oct. 1973	201	12	42	12	1	87	1
	181–248			(75)	(14)	(9)	(2)
Total	204	98	37	41	2	57	1
				(75)	(8)	(17)	(<1)

these numbers never exceeded 1% dry weight of the diet. Alewives were consumed most frequently during the June collection when yearlings composed 58% dry weight of the diet. Small alewives constituted 30 and 10% dry weight of the diet during August and October, respectively.

Food eaten by smelt 180 mm and longer consisted principally of small alewives and *Mysis*, but included small numbers of *Pontoporeia* and occasionally fingernail clams (Table 3). Yearling alewives represented 94 and 99% dry weight of the diet during the May and June collections, respectively.

Smelt examined for feeding periodicity averaged 158 mm total length. Weight of stomach contents differed statistically over the 24-h period during the October collection ($F = 9.99$, $P \leq 0.001$, df = 5, 82). Stomachs contained the most food (1.5% body weight) at 2430 h and decreased to 0.2% by 0400 h (Figure 1). In addition, the occurrence of empty stomachs was dependent upon time of day ($\chi^2 = 31.51$, $P \leq 0.001$, df = 5). Only 1 out of 45 stomachs was empty in the collections between 1600 and 2430 h. In contrast, 23 out of 43 stomachs were empty between 0400 and 1200 h (Figure 1). The March collection showed no significant differences in weight of stomach contents over a 24-h period.

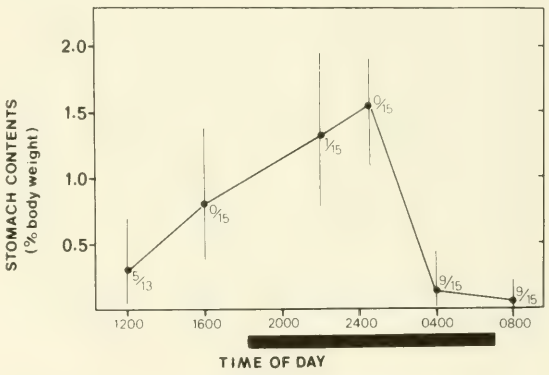

FIGURE 1.—Feeding periodicity of Lake Michigan smelt collected on 13–14 October 1973. Dry weights of stomach contents are expressed as a percentage of dry body weight. Vertical lines represent ±2 SE of the mean and the horizontal black bar the hours of darkness. The number of empty stomachs and number of stomachs examined are given near each average.

Discussion

Smelt examined in this study were piscivorous, consuming young-of-the-year and yearling alewives. Food habit studies of smelt in Saginaw Bay, Lake Huron (Gordon 1961) and Lake Erie (Price 1963) have shown that smelt consume fishes, but not alewives. Smith (1970) hypothesized that dif-

ferences in their depth distributions could explain failure to demonstrate predation of smelt upon alewives. Recently, smelt collected from northern Lake Michigan during the fall were reported to contain large numbers of young-of-the-year alewives in their stomachs (O'Gorman 1974). Smelt examined in this study consumed alewives not only during the fall, but also during February, May, June, and August. This study and O'Gorman's confirm the smelt's role as a predator of alewives in Lake Michigan. The high frequency of small alewives and *Mysis* in the diet of smelt suggests a preference for larger food items.

Increased piscivority with size is well known among predatory fishes. Lake Erie smelt longer than 126 mm consumed more fishes than smaller specimens (Price 1963). In this study, smelt 180 mm and longer consumed about three times more fish than the smaller individuals (grand averages of 57 and 23%, respectively). According to O'Gorman (1974), the smallest smelt which had consumed a fish was 143 mm total length. In the present study, the smallest smelt which had consumed an alewife was 157 mm.

Seasonal differences in food habits reflect changes in depth distribution of smelt and annual changes in abundance of prey. Smelt in Gull Lake, Mich., consumed primarily copepods and cladoceran during early winter but from May to August, dipterans were their principal food (Burbidge 1969). Similarly, smelt examined in this study consumed Tendipedidae only during May, June, and August, when the flies were abundant. In Lake Superior, smelt longer than 125 mm consumed mostly *Mysis* except during May and June, when copepods ranked first (Anderson and Smith 1971). Likewise, smelt examined in our study showed a change in food habits from winter to spring but, in this case, from *Mysis* to yearling alewives. Following littoral spawning during April, smelt were captured in shallower water where *Mysis* is not abundant. Schools of small alewives occupying this zone provided an alternative food.

Smelt examined during October fed after dusk and ceased feeding during the night. *Mysis* represented 87% dry weight of the diet during the October collection. This in conjunction with the known fact that *Mysis* undergoes a nocturnal vertical migration (Beeton 1960) suggests that their feeding was associated with the migration, and consequent availability of the smelt's principal food organism. Feeding of young-of-the-year sockeye salmon, *Oncorhynchus nerka,* has been related to diel vertical movements of zooplankton (Narver 1970). A statistically significant feeding periodicity was not demonstrated during the March collection. However, this could be due to reduced feeding intensity as evidenced by very small amounts of food present in their stomachs (e.g., 0.1% body weight).

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USEABLE MEAT YIELDS IN THE VIRGINIA SURF CLAM FISHERY[1]

The weight of surf clam meat landed in Virginia is estimated by the National Marine Fisheries Service, Division of Statistics and Market News (DSMN) by multiplying bushels landed by a constant of 17 lb (7.71 kg) of total meat per bushel. However, total meat weight includes the viscera, a portion of clam not utilized by the industry. Herein is an analysis of the yield of useable surf clam meat weight per bushel and seasonal variability in meat weight relative to seawater temperature for Virginia stocks.

Methods

Monthly mean useable meat weight per bushel (MMUWB) was estimated from 181 daily landings totaling 167,564 bushels in 1974, and 160 daily landings totaling 270,170 bushels in 1975. The surf clams were harvested from Virginia stocks in the region offshore of Cape Henry and south to about False Cape.

Meat weight landings reported by DSMN are in pounds, for conformity useable meat weight estimates are also cited in pounds.

Monthly mean seawater temperature (MMST) was estimated from daily surface water temperatures recorded at Kiptopeke Beach, Va. (lat. 37°10.0′N, long. 75°59.3′W), about 13 n.mi. north of Cape Henry. These data, collected and published by National Oceanic and Atmospheric Administration (NOAA), Oceanographic Surveys Branch, exhibited seasonal trends which were correlated to changes in useable meat yield per bushel. Although these temperatures are not in situ measurements, they are a convenient covariate of meat yield.

The relationship of MMUWB to MMST was estimated by Model II regression analysis since both variables were subject to sampling error. The choice of a particular Model II analysis relative to the source of the variability (measurement errors, inherent variability, or both) is a somewhat unsettled subject recently discussed by Moran (1971), Ricker (1973, 1975) and Jolicoeur (1975). No such theoretical considerations were used in the present analyses. Four models were employed to derive "predictive" equations from the 1974 data: Ricker's (1973) geometric mean analysis (GM regression); Wald's (1940) and Bartlett's (1949) arithmetic mean analysis (termed AM regression by Ricker); and principal axis analysis (although it is recognized that variables do not truly have a bivariate normal association). Empirically, the adequacy of the models in predicting the observed 1975 annual mean useable meat weight per bushel (AMUWB) from the MMST in 1975 was assessed by a randomized block (two-way) analysis of variance in which the predicted and observed MMUWB were the experimental units replicated by months. MMST was recorded to 0.1°C, MMUWB to 0.01 lb.

Results and Discussion

The MMUWB of surf clams ranged from 10.8 to 14.0 lb in 1974, and from 10.6 to 14.5 lb in 1975 (Table 1). AMUWB, 12.5 lb in 1974 and 12.6 lb in 1975, were nearly identical ($P>0.80$). There was a cyclical increase in the MMUWB from the minima in winter months to maxima in July and August 1974 and in July 1975. The correlation coefficients (r) for MMUWB and MMST were 0.64 and 0.79 in 1974 and 1975, respectively; $r = 0.71$ for the pooled data.

The sinusoidal trend in MMUWB is probably related to maturation and subsequent spawning. Ropes (1968) reported a major spawning period in summer and a minor period in fall in New Jersey waters, but the time and duration of surf clam spawning in Virginia waters has not been reported. If increasing MMUWB is indicative of maturation, the data imply that most spawning by

[1]Contribution No. 801, Virginia Institute of Marine Science, Gloucester Point, Va.

TABLE 1.—Number of bushels of surf clams processed, mean weight (pounds) of useable meats per bushel, and mean surface seawater temperature at Kiptopeke Beach by months in 1974 and 1975.

Month	Number of bushels		Mean useable meat/bushel		Mean seawater temperature (°C)	
	1974	1975	1974	1975	1974	1975
Jan.	19,736	18,225	11.7	10.6	6.7	5.9
Feb.	11,791	18,489	12.3	11.3	5.6	5.7
Mar.	13,450	8,237	12.3	12.7	8.4	6.7
Apr.	14,415	23,725	13.3	13.2	12.2	9.8
May	19,020	39,130	13.8	12.9	17.6	17.1
June	12,981	30,049	13.9	13.7	21.7	22.5
July	8,328	19,488	14.0	14.5	24.8	24.6
Aug.	10,140	23,930	14.0	13.7	25.0	26.6
Sept.	14,430	23,038	12.0	13.2	22.9	23.2
Oct.	14,558	29,136	11.4	12.4	16.2	19.5
Nov.	13,388	8,407	10.8	11.8	12.2	14.0
Dec.	15,327	28,316	10.8	11.1	6.8	7.6
Total	167,564	270,170				
Annual mean yield/bushel			12.52	12.59		

Virginia surf clams is from about May or June through August. Loesch[2] reported a size range of 2 to 18 mm for young-of-the-year surf clams in early October 1974 and estimated their age ranged from 1 to 4.5 mo. Thus, spawning in 1974 occurred from at least June through early September.

The regression of MMUWB on MMST for the 1974 data by the four models resulted in the following equations:

$$\text{Wald's AM regression: } \bar{W} = 10.1 + 0.102\,\bar{C}$$
$$\text{Bartlett's AM regression: } \bar{W} = 11.0 + 0.101\,\bar{C}$$
$$\text{Ricker's GM regression: } \bar{W} = 10.0 + 0.168\,\bar{C}$$
$$\text{Principal axis: } \bar{W} = 10.9 + 0.108\,\bar{C}$$

where $\bar{W}$ = MMUWB; $\bar{C}$ = MMST (degrees Celsius); and the first and second values are the intercept and regression coefficients, respectively.

Predicted MMUWB values in 1975 and their respective AMUWB are presented in Table 2. Analysis of variance (Table 3) indicated a significant difference among the predicted and observed AMUWB values ($P<0.001$). The Student-Newman-Keuls multiple range test indicated that the only significantly different AMUWB was that associated with the predicted MMUWB estimates derived from Wald's AM regression. Thus, the other three regression models predicted the AMUWB with equally acceptable precision.

The total useable meat yield obtained from the 270,170 bushels of surf clams processed in 1975 was 3,425,654 lb (1,554 metric tons). The sum of the products of MMUWB and monthly landings

[2]Loesch, J. G. 1975. Inventory of surf clams in nearshore waters from Cape Henlopen to the False Cape area. Final Rep. 03-4-043-357, U.S. Dept. Commerc., Natl. Mar. Fish. Serv., State–Fed. Fish. Manage. Prog.

TABLE 2.—Mean monthly useable meat weight (pounds) per bushel for Virginia surf clams in 1975 estimates by four regression models.

Month	AM (Wald)	AM (Bartlett)	GM (Ricker)	Principal axis
Jan.	10.7	11.6	11	11.5
Feb.	10.7	11.6	11	11.5
Mar.	10.8	11.7	11.1	11.6
Apr.	11.1	12.0	11.6	12.0
May	11.8	12.7	12.9	12.8
June	12.4	13.3	13.8	13.3
July	12.6	13.5	14.1	13.6
Aug.	12.8	13.7	14.5	13.8
Sept.	12.5	13.4	13.9	13.4
Oct.	12.1	13.0	13.3	13.0
Nov.	11.5	12.4	12.4	12.4
Dec.	10.9	11.8	11.3	11.7
Annual mean yield/bushel	11.65	12.55	12.57	12.55

TABLE 3.—Randomized block analysis of variance of the 1975 observed and predicted mean monthly useable meat weight (pounds) per bushel replicated by months.

Source of variation	Degree freedom	Sum of squares	Mean square	Critical ratio (F)
Months	11	50.96	4.63	
Among models	4	7.97	1.99	
Within models	44	6.84	0.155	12.83*
Total	59	65.77		

*$P<0.001$

for all three acceptable models estimated the total useable meat yield with an error ≤0.5%. For all practical purposes the estimate could have been made by using the 1974 AMUWB of 12.5 lb. Total useable meat estimated with this constant was in error by only 1.4%. However, because of seasonal changes in body weight, monthly total useable meat yields should be derived from the MMUWB predicted by one of the acceptable regression equations.

The observed AMUWB for the pooled data of 1974 and 1975 is 12.55 lb and can be used if only annual estimates of useable surf clam meat yields for Virginia stocks are desired. If a substantial change in seasonal harvesting occurred, e.g., a closed season, one of the acceptable regression equations should be used until a new AMUWB constant is estimated.

Barker and Merrill (1967) reported losses of 11 to 20% in body weight with the removal of the viscera from New Jersey surf clams. However, they sampled in May and November when the gonadal portion of the viscera is not near its maximum weight. The present data indicate that the reported DSMN yearly landing weights, based on 17 lb of meats per bushel, must be reduced by 26% to more accurately ascertain the weight of Virginia surf clam meats actually shipped to market.

Acknowledgments

I am indebted to Ned Doughty, owner and operator of the C&D Seafood Company, Oyster, Va., who made available his daily surf clam landing and meat yield data for 1974 and 1975. Also, I acknowledge the aid of Charles R. Muirhead, Chief, Oceanographic Surveys Branch, NOAA, who supplied the monthly mean seawater temperature data for Kiptopeke Beach, Va., prior to its publication.

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MERCURY IN FISH AND SHELLFISH OF THE NORTHEAST PACIFIC. III. SPINY DOGFISH, *SQUALUS ACANTHIAS*

The spiny dogfish, *Squalus acanthias* Linnaeus, is a small shark that is abundant in the northeast Pacific and has been utilized both as a food fish and as a source of industrial fishery products. This species was heavily harvested in the 1940's for the high vitamin A content in the liver oil until the population was significantly reduced (Alverson and Stansby 1963). The declining resource, along with the availability and low cost of synthetic vitamin A, led to the collapse of the fishery in the early 1950's. Since that time the dogfish population has significantly increased, but the low economic value of the species precluded development of any substantial fishery.

Another limiting factor in commercial handling of dogfish is its rather rapid deterioration. Stansby et al. (1968) found that rancidity, not bacterial spoilage, was the principal factor limiting the ice-storage life of dogfish. If dogfish are properly iced and handled quickly, off flavors due to rancidity and the breakdown products of urea are minimized, and they can be used as food.

Recently there has been a renewed interest in commercial exploitation of this species in Puget Sound, primarily because of the export demand and increased price for frozen dogfish fillets and bellyflaps in Europe. In 1975 only 0.43 million lb of dogfish were landed in the State of Washington for both food and reduction purposes, in contrast to 4.9 million lb landed during 1976 in Puget Sound ports[1] and processed for export to Great Britain and West Germany. As a result of the current interest in the use of Puget Sound dogfish as food and the mercury levels in relation to import regulations of various countries, this investigation was undertaken to determine the mercury levels in dogfish from inland waters of the State of Washington. This report summarizes our findings.

Materials and Methods

The specimens were obtained from commercial gill net and longline catches through the cooperation of the industry and the State of Washington Department of Fisheries. They were collected from the Strait of Georgia near Blaine, Wash. (Figure 1), and from five locations in Puget Sound: Port Townsend, Port Susan, Seabeck (Hood Canal), Seattle (Elliott Bay), and Tacoma (Tacoma Narrows to Carr Inlet). Date and location of capture, round weight, length, and sex were recorded for each fish. Commercial buyers had established a minimum acceptable length of 32 in (81.3 cm) for food processing; therefore, the size distribution of most samples reflected this market practice rather than the normal range of lengths in the dogfish population.

[1]Preliminary landings data, State of Washington Department of Fisheries.

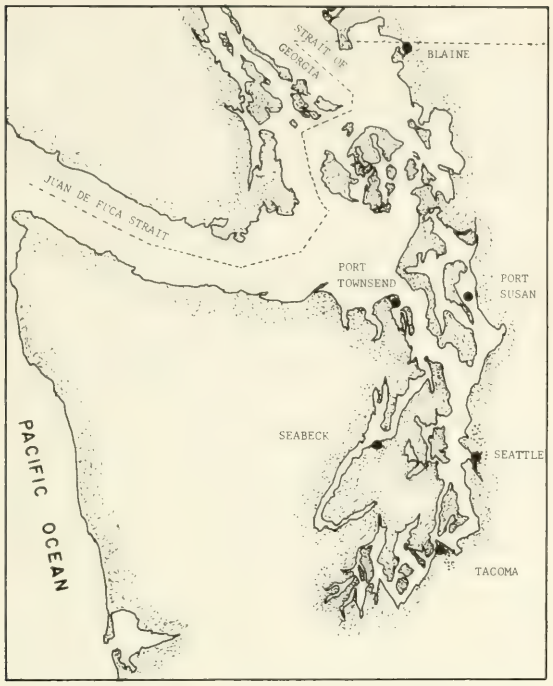

FIGURE 1.—General points of collection of spiny dogfish in Puget Sound and the Strait of Georgia.

Analytical samples were prepared at this laboratory and consisted of the skinned and deboned edible muscle tissue from both fillets and bellyflaps. Since the bellyflaps are marketed as a separate product, they were removed and analyzed separately. Each sample was ground and thoroughly mixed prior to subsampling for analysis.

Total mercury was determined by the U.S. Food and Drug Administration's Vanadium Pentoxide Method (Munns 1972), which uses a nitric-sulfuric acid digestion with vanadium pentoxide as a catalyst. Final determination was by flameless atomic absorption spectroscopy with results stated in parts per million (ppm) of mercury on a wet-weight basis. All samples were subjected to single analysis, and those exceeding 0.40 ppm were repeated. Differences between replicates did not exceed 0.05 ppm. A standard fish sample was analyzed routinely as an internal control.

Results and Discussion

A total of 141 dogfish (127 females, 14 males) were analyzed for mercury content. Mean mercury levels in specimens from each area (Table 1) were at or above the action level of 0.50 ppm set by the U.S. Food and Drug Administration (FDA) (Schmidt 1974). Specimens taken from the west side of Puget Sound (Port Townsend and Seabeck) contained lower levels of mercury than did those taken from the east side of Puget Sound (including Blaine). The mercury levels appeared to increase from north to south on each side of the Sound. This phenomenon may be due to the absence of industry at points of collection on the west side of the Sound and an increase of industrial activity from north to south along the east side of the Sound; however, these observations on the effect of catch area may not be representative of the total Puget Sound dogfish population.

The mean mercury level for the 127 female dogfish fillets was 0.92 ppm, which is almost twice the FDA action level. The mercury level in 91 females (72%) exceeded 0.50 ppm and 48 (38%) exceeded 1.0 ppm. Regression analysis showed a positive correlation between mercury content of

TABLE 1.—Mercury concentration in spiny dogfish from the State of Washington.

						Mercury (ppm)										
						Fillets					Bellyflaps					
		Weight (g)		Length (cm)					>0.5 ppm						>0.5 ppm	
Location	No. of fish	Range	Mean	Range	Mean	No. of fish	Range	Mean	No.	%	No. of fish	Range	Mean	No	%
						Females									
Port Townsend	22	2,190–4,160	3,194	85–102	93 9	22	0.16–1.28	0.50	9	40.9	20	0.14–1.18	0.41	5	25.0
Seabeck	12	2,465–4,915	3,372	86–106	93.5	12	0.34–1.43	0.63	7	58.3	12	0.29–1.30	0.57	7	58 3
Blaine	20	2,360–5,065	3,469	86–106	94.6	20	0.20–1.38	0.71	15	75.0	20	0.17–1.27	0.62	15	75.0
Port Susan	32	1,340–4,560	3,033	70–106	89.6	32	0.09–2.28	0.89	20	62.5	22	0.17–1.95	1.02	19	86.3
Seattle	8	5,230–7,930	6,706	105–117	109.9	8	0.82–1.94	1.16	8	100 0	—	—	—	—	—
Tacoma	33	700–6,630	3,862	60–113	95.2	33	0.43–2.58	1.41	32	96.9	33	0.38–2.24	1.25	32	96 9
Σ	127	700–7,930	3,608	60–117	94.2	127	0.09–2.58	0.92	91	71.6	107	0.14–2.24	0.85	78	72.9
						Males									
Port Susan	7	1,445–2,645	1,864	75–87	79.4	7	0.21–0.98	0.64	6	85.7	2	0.49–0.95	0.72	1	50.0
Seattle	4	2,025–3,400	2,626	85–93	89.0	4	1.16–1.61	1.38	4	100.0	—	—	—	—	—
Tacoma	3	1,240–2,180	1,728	68–84	77.3	3	0.94–1.27	1.15	3	100.0	3	0.92–1.24	1.08	3	100 0
Σ	14	1,240–3,400	2,052	68–93	81.7	14	0.21–1.61	0.96	13	92.8	5	0.49–1.24	0.93	4	80.0

the fillets and fish weight for the 127 females (Figure 2). The weight of individual fish was evenly distributed in each of the area samples with the exception of the small sample of eight fish from Seattle. Although these were the largest fish collected, they contained less mercury than smaller fish from other areas. The Seattle sample does not appear to be adequate in number and may not be representative of the population. In all areas, except Seattle, the correlation coefficients were significant for the relationship of mercury content to weight (Table 2). The correlations between mercury content and fish length were significant but slightly lower in four of the five groups showing

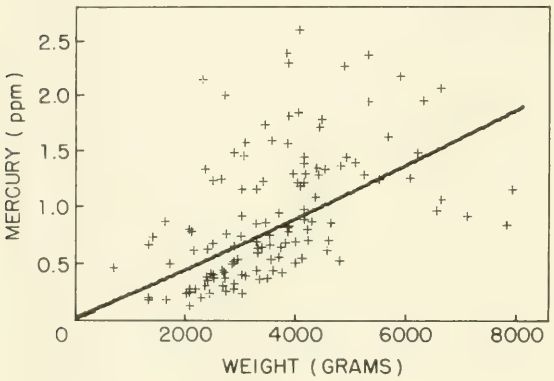

FIGURE 2.—Relationship between weight and mercury concentration in female dogfish fillets.

TABLE 2.—Correlation coefficients (r) and significance level (α) of mercury content to the weight and length of female spiny dogfish fillets from the State of Washington.

Location	No. of fish	Weight vs. mercury		Length vs. mercury	
		r	α	r	α
Port Townsend	22	0.645	0.01	0.507	0.05
Seabeck	12	0.648	0.05	0.616	0.05
Blaine	20	0.768	0.001	0.756	0.001
Port Susan	32	0.699	0.001	0.643	0.001
Seattle	8	0.501	NS[1]	−0.414	NS
Tacoma	33	0.601	0.001	0.648	0.001
Σ	127	0.576	0.001	0.530	0.001

[1]Not significant

positive coefficients. We expected a more significant correlation with length, since the weight of the females varied as to whether or not they were pregnant and the length of gestation. Childs et al. (1973) stated that mercury is not concentrated in the fetuses in situ; therefore, the mercury level in the flesh of the female is presumably unaffected by pregnancy.

The bellyflaps of 107 female and 5 male dogfish were analyzed (Table 1). Bellyflaps of the fish from Seattle and 10 small females from Port Susan were not analyzed. The bellyflaps contained slightly less mercury than the corresponding fillets; however, the percentage exceeding the action level (73%) was not significantly different from that for fillets.

The limited data on mercury levels in male dogfish (Table 1) indicated that essentially all male dogfish over the minimum commercial size (81.3 cm) would exceed the FDA action level. Of the 14 males analyzed, 13 (93%) exceeded the action level. The mean weight of the males (2,052 g) was less than the mean weight of the females (3,608 g), yet the mean mercury level was higher (0.96 ppm for males and 0.92 ppm for females). This difference may be attributed to the fact that males are smaller than females of the same age (Jensen 1966). Our findings agree with those of Forrester et al. (1972) on the mercury levels in male and female spiny dogfish from inland waters of British Columbia.

A study by Childs and Gaffke (1973) included 88 dogfish taken off the Oregon coast and showed a similar correlation of mercury level to weight and length but a lower mean level of 0.602 ppm mercury in all muscle samples. This suggests that dogfish taken from the Pacific Ocean off the Oregon coast may contain less mercury than the population sampled in this study of the inland waters of Washington. Tagging studies by Kauffman (1955) and Holland (1957) indicated that offshore dogfish populations may be highly migratory. Jensen (1966) noted that the nature of the dogfish's seasonal migration in offshore coastal waters was not clearly understood. Alverson and Stansby (1963) stated that the dogfish within Puget Sound show less tendency to migrate and that Puget Sound stocks are apparently somewhat independent from the coastal and offshore stocks. They further stated that some movement of dogfish may occur between ocean areas and Puget Sound. The mercury levels found in our study are most probably those of a population indigenous to Puget Sound.

Acknowledgments

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LOCALIZED MASS MORTALITY OF RED SEA URCHIN, *STRONGYLOCENTROTUS FRANCISCANUS*, NEAR SANTA CRUZ, CALIFORNIA

Johnson (1971) reported on the occurrence of a mass mortality of red sea urchin, *Strongylocentrotus franciscanus* (Stimpson 1857) off Point Loma, San Diego, in the summer of 1970, and she detailed the symptoms of the diseased sea urchins. Large areas of the test, particularly of the interambulacra, were denuded of spines and epidermis. These denuded areas were chalky white with green blotches and often were bordered by a ring of swollen tissue. The test plates of the denuded area were layered and a middle "red-friable" layer with disorganized cellular structure replaced the normal plate tissue and ossicle. In some cases, lesions broke through the denuded tests and these apparently led to the animals' death. The internal organs appeared to be normal. Johnson (1971) was unable to determine the cause of these symptoms, but she suggested that a microorganism, perhaps a fungus, might be responsible.

The area affected in the 1970 mass mortality off Point Loma was limited to a few hectares (Johnson 1971). It was first noted in May 1970, when the center of the area was littered with dying sea urchins while the perimeter had fewer diseased animals with only small patches of denuded tests. The affected area did not spread, and by the middle of summer, many of the surviving urchins were regenerating spines. Diseased animals with partially denuded tests were difficult to find in November 1970.

We report here two other localized mass mortalities of *S. franciscanus* in central California, which seem to be similar to the one documented by Johnson (1971). One was found in 3–5 m of water off the southeast side of Año Nuevo Island (lat. 37°06′25″N, long. 122°19′30″W). It was first observed on 18 July 1976, and revisited on 31 July 1976. Diseased animals with drooping spines and partially denuded tests were found scattered among healthy-appearing individuals. They did not seem to be clumped or segregated, although most diseased animals were in the open while healthy-appearing animals tended to be under ledges or in crevices. Diseased animals did not hold onto the rocks as normal animals usually do, and they were picked up easily by divers. Empty tests of recently dead animals littered portions of the bottom. Red sea urchins were the only animals noted to be affected at the Año Nuevo Island site. Other areas of similar depth to the south and northwest of Año Nuevo Island supported numerous healthy-appearing red sea urchins and none with denuded tests.

The diseased animals collected from Año Nuevo Island were very similar to those described by Johnson (1971) (Figure 1). Portions of the test were denuded of spines while the remainder of the test was covered with normal-appearing spines. The affected test plates were layered with a thin greenish surface layer, a red-friable middle layer

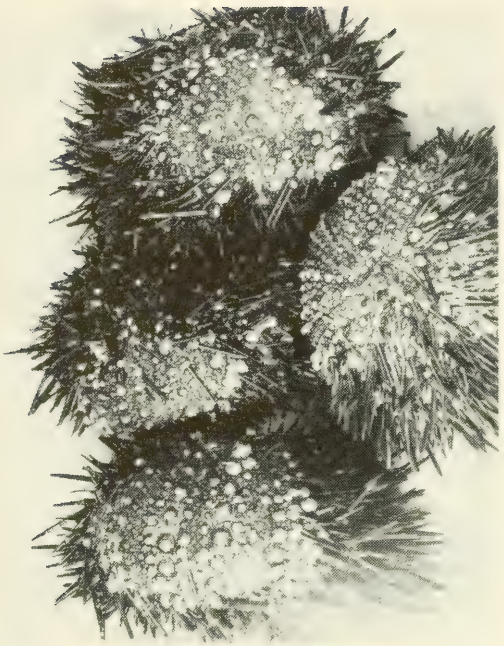

FIGURE 1.—Four diseased *Strongylocentrotus franciscanus* collected on 31 July 1976 from 3–5 m depth off Año Nuevo Island, Calif. Each animal is about 10 cm in diameter. Note the large portion of test denuded of spines in each animal.

and a nearly normal white inner layer (the "callus" layer, see Pearse and Pearse (1975) for description of the layers of the test plates and methods for examining them). Portions of the inner layer of the affected area were discolored reddish brown, however, often with a rather blotchy appearance. Clorox[1] cleaned and thin-ground preparations of the plates showed that middle layer of the diseased plates had lost much of its trabecular structure and there were large spaces between the middle layer and the inner layer. In the most diseased plates, the inner layer could be separated easily from the middle layer of the plates. The ambulacral system with the water vascular canals, ampullae, and radial nerve were all discolored reddish brown under the diseased portions of the test and much of these tissues were speckled with dark reddish-brown flakes, probably clumped coelomocytes. The internal organs in other portions of the diseased animals appeared normal.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The symptoms noted in the diseased animals at Año Nuevo Island in 1976 seemed identical to those described for diseased animals found at Point Loma in 1970 by Johnson (1971). Such similarity suggests that the same disease organism may be involved in these mass mortalities. Alternatively, the symptoms could reflect a general response to localized infections or disruptions of the test from a variety of physical, chemical, or biological agents. As Johnson (1971) cautioned, careful microbiological work needs to be done before the causative agent(s) of these mass mortalities can be identified.

The Año Nuevo Island site of the mass mortality was revisited on 24 September 1976. Sea urchins were scarce compared with the earlier visit and most were nestled in crevices. Only one animal was found with symptoms of the disease; it had a narrow strip down one interambulacrum which was denuded of spines. However, when this animal was examined in the laboratory, it was found that a large portion of the diseased interambulacrum and adjacent ambulacrum was covered with short regenerating spines, and the ambulacrum was concave and grossly deformed. Six other normal-appearing animals were brought into the laboratory and two of these had small areas on the test with regenerating spines. From these observations, it appeared that the mass mortality had ceased and some of the animals survived and regenerated their lost spines.

The second mass mortality of *S. franciscanus* we found in 1976 occurred at 4–6 m depth off the east side of Point Santa Cruz (lat. 36°57′05″N, long. 122°01′30″W); this area was described by Mattison et al. (1977). Animals looking "sick" and losing spines were seen in the area in early June (A. L. Shanks, J. D. Trent pers. commun.). We did quantitative studies at fixed stations off Point Santa Cruz on 28–30 June 1976 and again on 10–11 September 1976. Although we found no animals with denuded tests at our study stations, there was a notable decrease in the number of animals present compared with the counts made in the previous two summers (Figure 2). The number of animals at the seaward edge of the kelp forest maintained densities of about 55–65/10 m^2 during the summers of 1974 and 1975. Fifty and one hundred meters seaward of the kelp forest, lower densities of 20–30 animals/10 m^2 occurred on the barren-appearing rocks. In the summer of 1976, we found only about 20 animals/10 m^2 at the edge of the kelp forest and about 1–2/10 m^2 50 and 100 m

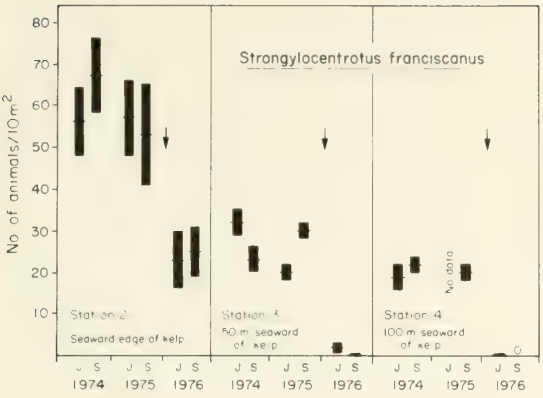

FIGURE 2.—Densities of *Strongylocentrotus franciscanus* at three fixed stations off Point Santa Cruz as estimated in June and September 1974, 1975, and 1976. Each station encompassed an area of 2,500 m² and the density estimates are based on counts from 12 randomly selected 10 m² quadrats. Station 1 was located 50 m inshore from Station 2 within the kelp forest and always contained very low densities of sea urchins, <1/10 m². Figure shows mean number of animals per 10 m² and the standard error of the mean. The arrows indicate the period of the mass mortality.

offshore. This represents a decrease of about 60% of the dense population of animals at the kelp forest edge and about 95% of the animals farther offshore. The area of each study station was about 2,500 m². In absolute terms, the decrease in number of animals within the study station at the edge of the kelp forest was about 9,000 animals, while in each of the two study stations 50 and 100 m farther offshore, about 5,500 animals were lost.

About 10% of the animals remaining in our Point Santa Cruz study site in June 1976 had large conspicuous portions of the test covered with regenerating spines only 1–5 mm long, contrasting noticeably with the surrounding normal-appearing areas. Since we did not detect any abnormalities in January 1976, the mass mortality probably followed its full course in less than 6 mo, as did the one described by Johnson (1971), and probably the one we observed at Año Nuevo Island.

During August–October 1976 we (M. B. Y. and C. R. A.) surveyed the 35-km coastline between Point Santa Cruz and Año Nuevo Island at 2-km intervals. Most of the kelp forests along this coastline have dense populations of *S. franciscanus* along their seaward edge, similar to conditions found at Point Santa Cruz before 1976. No evidence of mass mortality of these populations of sea urchins was found, either as large numbers of dying animals or unusually low numbers of animals. However, diseased animals with partially denuded tests were found occasionally all along the coastline with estimated incidences of 1 in 1,000 animals. These observations suggest that potential outbreaks of localized mass mortalities could occur in many places under suitable conditions.

The mass mortality of *S. fransicanus* at Point Loma in 1970 and those at Año Nuevo Island and Point Santa Cruz in 1976 were all relatively small and localized in both space and time. Moreover, all the animals in the populations were not killed. Rather, within less than 6 mo low numbers of normal and healthy-appearing animals were present and there was little trace of the mass mortalities—no piles of empty tests remained. Small localized mass mortalities might occur in other areas and not be noticed or reported. If they do, such mass mortalities could be important in regulating the distributions and densities of sea urchin populations. Moreover, since a major portion of the recruitment of juveniles of *S. franciscanus* occurs under adult animals (Tegner and Dayton 1977), near complete mass mortalities, such as that in our study stations 50 and 100 m seaward of the kelp forest off Point Santa Cruz, could have long lasting effects. Such a source of mortality could have practical importance both as means of minimizing overgrazing of kelp by sea urchins (North and Pearse 1971) and as a threat to the developing sea urchin fishery in California (Kato 1972).

Acknowledgments

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FIRST RECORD OF A SECOND MATING AND SPAWNING OF THE SPOT PRAWN, *PANDALUS PLATYCEROS*, IN CAPTIVITY

The spot prawn, *Pandalus platyceros* Brandt, is the largest species of the family Pandalidae. It supports a minor fishery within its range of San Diego to the Bering Strait, Korea, and Japan in depths to 532 m (Butler 1964). The prawn is being studied at the National Marine Fisheries Service (NMFS) Aquaculture Research Station, Manchester, Wash., as a possible companion crop to Pacific salmon reared in floating net pens (Mahnken 1975; Prentice 1975). One phase of this work is to investigate the reproductive potential of the prawn in captivity.

The prawn is a protandric hermaphrodite, i.e., an individual matures first as a male (at age 1.5 yr), breeds one or more times as a male, passes through a transitional phase (at age 2.5 yr), and becomes a functional female (at age 3.5 yr) (Butler 1964). In studies of natural populations in southern British Columbia, Butler (1964) found that few if any females breed more than once and suggested that the females die soon after spawning.

At the Aquaculture Research Station, prawn culture and breeding experiments have been carried out since 1973. The matings reported in this study were made with laboratory-cultured males and captured, wild females. The females were captured in ovigerous condition in 1974 from Hood Canal, Wash., and their eggs hatched in the laboratory during February and March 1975. Therefore, we know these females have spawned at least once, and since their prior history is unknown, there is the possibility that some or all may have spawned more than once.

The spawned females (103) were held from March to August at the Aquaculture Research Station in floating net pens or in benthic cages 10 m beneath floating net pens containing salmon. The postspawning survival was 100% through August 1975 for both groups. All prawns in the net pens were maintained on a diet of frozen clam meat, *Panope generosa*, and salmon mortalities. The benthic cage group did not receive any supplemental food.

In August varying densities of spawned females and cultured males (Table 1) were placed either in three net pens, eight laboratory tanks, or in a benthic cage. The net pens were constructed of 18-mm mesh (stretch measure) knotless nylon with 6.8 m^2 of substrate per pen available to the prawns. The top of each pen was covered with black plastic sheeting. Each laboratory tank had 0.24 m^2 of available substrate. All water entering the tanks was sand filtered and not recycled. The single benthic cage was constructed of vinyl-coated wire mesh (9.0-mm stretched measure) and had 2.6 m^2 of substrate available to the prawns. All test groups were fed the clam–salmon diet with the exception of those in the benthic cage which received no supplemental food. A continuous low-level mortality was observed among the females from August to early October 1975 which reduced their survival to 39.8%.

Survival of the female prawns was not dependent upon stocking density; however, survival was significantly greater in the benthic cage and laboratory tanks than in the net pens (Table 1).

TABLE 1.—Survival (percent in parentheses) and second spawning of female *Pandalus platyceros* in three seawater systems.

Container type	No. of prawns per container		Density of prawns[1]	Survival of previously spawned females	Survivors spawning a second time
	Female	Male			
Benthic cage (9 m deep)	5	5	3.8	4 (80.0)	3 (75.0)
Net pen 1	29	56	12.5	12 (44.8)	10 (84.6)
Net pen 2	24	43	9.9	6 (25.0)	4 (66.7)
Net pen 3	29	89	17.4	6 (20.7)	5 (83.3)
Laboratory tanks[2]	2	2	16.7	12 (75.0)	12 (100.0)

[1]Prawns per square meter of available substrate.
[2]A total of eight laboratory tanks.

Females held in the bottom cage or in the laboratory tanks were subject to less ambient light, more stable temperatures, and water below the photosynthetic zone. The laboratory water system utilizes water pumped from an area 2 m above the sea floor, thereby approximating the water available to the bottom caged prawns. Previous work has shown that juvenile and yearling prawns are sensitive to rapidly fluctuating water temperature, light, and plankton blooms (Rensel and Prentice[1]).

A second spawning was recorded for 85.4% of the surviving females. The average carapace length of these spawners was 39.2 mm (SD = 1.31). Eggs developed normally, producing viable larvae, but the fecundity was low, ranging from 10 to 1,000 eggs. The fecundity of wild bred stocks is 2,000–5,000 eggs per female. The reduced fecundity in the female prawns spawning for the second time may be due to nutritional or environmental factors. However, in some instances the female prawns were observed actively removing eggs from their own abdomens, using the second pereiopod. In other cases, we observed egg losses during the holding period due to abrasion on the nets and tanks.

Multiple breeding and spawning are common in other families of caridean shrimps, but among the Pandalidae only *P. montagui* Leach in the northeastern Atlantic Ocean has been known to spawn for two consecutive years (Allen 1963). This study shows that female spot prawns can also successfully breed, spawn, and hatch eggs for a second time. This is important to both the aquaculturist and the field biologist. If multiple breeding also takes place in wild populations, then estimates of year-class recruitment based on single spawning populations are in error.

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[1]Rensel, J. E., and E. F. Prentice. A comparison of growth and survival of cultured spot prawns, *Pandalus platyceros* Brandt, at two salmon farming sites in Puget Sound. Unpubl. Manuscr., 25 p. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash.

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EFFECT OF DISSOLVED OXYGEN CONCENTRATION AND SALINITY ON SWIMMING SPEED OF TWO SPECIES OF TUNAS

Studies on captive skipjack tuna, *Katsuwonus pelamis,* have determined three physiological parameters that may operate to delimit oceanic distribution of this fish. If 1) a lower temperature limit of 18°C, 2) a size-dependent upper temperature limit, and 3) a lower oxygen limit of 5 ppm are mapped onto the temperature and oxygen levels of the central Pacific area, the resulting model is consistent with many of the peculiar features of the geographical distribution of the skipjack tuna (Barkley et al.[1]). In particular, the exclusion of adult skipjack tuna from warm, oxygen-poor waters of the eastern tropical Pacific Ocean is explained.

But the physiological parameters used in the model were either speculative—upper temperature limits—or based upon acute and stressful experimental conditions—lower oxygen and temperature limits. Gooding and Neill[2] determined the lower oxygen limit by introducing tunas into a small tank (1.8 × 2.4 × 0.6 m oval) containing

[1]Barkley, R. A., W. H. Neill, and R. M. Gooding. Skipjack tuna habitat based on temperature and oxygen requirements. Manusc. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812. (Material presented at 26th Tuna Conference, Lake Arrowhead, Calif., 29 Sept.–1 Oct. 1975.)

[2]Gooding, R. M., and W. H. Neill. Respiration rates and reactions to low oxygen concentrations in skipjack tuna, *Katsuwonus pelamis*. Manusc. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.

seawater at a given level of oxygen saturation. Swimming speed and survival time were measured. They found that survival time and swimming speed were independent of oxygen levels in excess of 4 ppm; below 4 ppm survival time was directly and swimming speed inversely proportional to dissolved oxygen amounts. So apparently 4 ppm is close to the incipient lower lethal limit for skipjack tuna under the given experimental conditions. For modeling distribution limits, Barkley et al. (see footnote 1) used a more conservative figure of 5 ppm.

However, a physiological limit of 4 or 5 ppm is not necessarily a behavioral limit; if the limit is approached slowly under natural and otherwise unstressful conditions, can a fish adaptively respond? Whitmore et al. (1960) found that coho salmon, *Oncorhynchus kisutch,* avoided water of lowered oxygen levels yet which produced no respiratory distress. In contrast, kawakawa, *Euthynnus affinis,* a species closely related to skipjack tuna, tolerated 2-ppm water for short periods in order to get food (Chang and Dizon[3]).

In the present experiment, I tested the responses of free-swimming tunas—both skipjack tuna and yellowfin tuna, *Thunnus albacares*—encountering slowly changing oxygen levels. The rate of change was comparable with that which a tuna might encounter in nature. Yellowfin tuna were tested for comparison because they are abundant in the same areas of the eastern tropical Pacific avoided by large skipjack tuna. Finally, salinity fronts have been suggested as a factor determining distribution, so responses to decreasing salinity levels were also examined.

Materials and Methods

Eight skipjack tuna and three yellowfin tuna were tested with decreasing oxygen levels, and three skipjack tuna, and one yellowfin tuna were tested with decreasing salinity levels. Fish were chosen from stocks at the Kewalo Research Facility of the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, Hawaii. Tuna stocks for this experiment were kept in outdoor tanks (7.3 m diameter × 1.2 m deep) until used; they were then removed by angling with a barbless hook and transferred to the swim chamber in a plastic bag partially filled with water. This is a good transfer technique since fish on occasion have fed immediately after transfer.

The responses of tunas to decreasing oxygen and salinity levels were examined in a tank system consisting of a swim chamber equipped with photocells for monitoring and recording fish behavior. (For details see Dizon et al. 1977.) The swim chamber was a 6.1 m diameter × 0.61 m deep fiber glass tank fitted with a concentric inner wall so the fish was constrained to swim in a 0.75-m channel around the periphery. Six laps equaled 100 m. Water (24°C) was introduced and removed from the swim channel through two pairs of concentric rings of polyvinyl chloride pipe. Entering (or exiting) water divided equally into two inflow (or outflow) pipes, each flowing countercurrent to the other to provide minimum oxygen or salinity asymmetry and horizontal transport of water within the swim channel. Water was recirculated through an outside circuit at 1,136 liters/min to insure thorough mixing of any introduced new water. New seawater was added to the tank at 38 liters/min.

Oxygen was reduced in the tank by replacing the 38 liters/min new seawater with 38 liters/min anoxic seawater obtained at our well head before aeration and introduced into the intake of the 1,136 liters/min recirculation pump. Oxygen decreased approximately exponentially within the swim chamber—0.06 ppm/min after 30 min and 0.03 ppm/min after 60 min. Salinity levels in the swim chamber were reduced by introducing aerated freshwater (38 liters/min) into the pump intake. Salinity decreased exponentially—0.07‰/min after 30 min and 0.03‰/min after 60 min.

Passage of the fish was sensed at four photocell stations (six photocells/station) at 90° intervals around the periphery of the swim channel. Information from the photocells was translated into swimming speed (minutes per lap), direction (clockwise or counterclockwise), and frequency of reversals or swimming direction by digital logic equipment and printed on adding machine tape.

Procedures were quite simple; tuna (starved for 1 day) were moved into the tank and allowed 100 min to habituate; swimming speeds were continuously recorded to provide baseline data to compare with behavior during periods of changing oxygen or salinity. After 100 min, a test was started and behavior was recorded as salinity or oxygen decreased. Oxygen and salinity levels were allowed

[3]Chang, R. K. C., and A. E. Dizon. Low oxygen levels as barriers to voluntary movements of tunas. Manusc. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812. (Material presented at 26th Tuna Conference, Lake Arrowhead, Calif., 29 Sept.–1 Oct. 1975.)

to reach 2 ppm and 29‰, respectively. After reaching these levels (about 200 min), test water was shut down and normal seawater restored. The following morning fish were removed, weighed, and measured, and survivors were returned to holding tanks. Oxygen and salinity levels were monitored by oxygen meter and salinograph; samples were taken periodically for laboratory analysis to verify the instruments.

Results and Discussion

Behavioral responses to decreasing levels of salinity were unremarkable; Table 1 summarizes results from three skipjack tuna and one yellowfin tuna. No consistent swimming speed changes were observed during periods when salinity decreased from about 34‰ to 29‰. Although sample size is small, these tunas did not make any dramatic response to salinity changes of magnitudes expected within their normal habitat.

Figure 1 illustrates typical results from tunas encountering slowly changing oxygen concentration. At or about 4 ppm, skipjack tuna (Figure 1a) demonstrated an abrupt increase in swimming speed. In most fish tested, speed increased to over 2 lengths/s. Yellowfin tuna, in contrast, showed no alteration in swimming speed as oxygen levels decreased (Figure 1b).

Figure 2 summarizes the oxygen experiment observations from eight skipjack tuna and three yellowfin tuna. Individual points plotted are median swimming speeds for the eight skipjack tuna grouped by: 1) before treatment and 2) 1-ppm dissolved oxygen intervals both decreasing and increasing, i.e., 6–5, 5–4, 4–3, 3–2, and 2–3, 3–4, 4–5, 5–6. Number of swimming speeds sampled ranged from under 5 to over 100 depending on the number of laps swum during each interval. Heavy line connects the grand median of each interval. Similar data for each yellowfin tuna (decreasing oxygen intervals only) are included for comparison.

TABLE 1.—Effect of decreasing salinity on mean swimming speed in tunas.

Item	n	$\bar{X}$ (length/s)	SD
Skipjack tuna 1 (38.3 cm, 925 g)			
Before salinity change	28	2.10	0.40
During salinity change	22	1.82	0.40
Skipjack tuna 2 (37.7 cm, 882 g)			
Before salinity change	44	2.03	0.26
During salinity change	12	2.37	0.19
Skipjack tuna 3 (42.0 cm, 1,352 g)			
Before salinity change	30	1.21	0.07
During salinity change	15	1.16	0.06
Yellowfin tuna 1 (45.3 cm, 1,491 g)			
Before salinity change	39	1.54	0.30
During salinity change	31	1.81	0.26

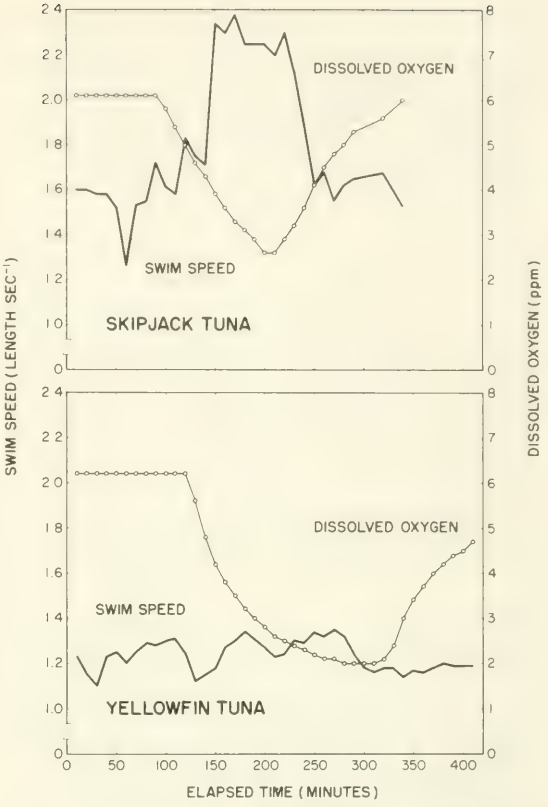

FIGURE 1.—Effect of dissolved oxygen level on swim speed in two species of tunas. Swim speeds are median values sampled for 10-min periods.

Not all of the skipjack tuna survived the treatment; three of the eight died when oxygen levels dropped below about 2.5 ppm. Survival times for skipjack tuna under conditions of low oxygen are as follows: in excess of 240 min at 4 ppm, 59 min at 3 ppm, and 18 min at 2 ppm (Gooding and Neill see footnote 2). My data are consistent with this resistance–time distribution, and both studies support the Barkley et al. (see footnote 1) hypothesis that there does exist a low oxygen level that limits the observed oceanic distribution of skipjack tuna.

Yellowfin tuna are not apparently stressed during the exposures to the low oxygen water employed. In separate tests done after the exposures to decreasing oxygen, two additional yellowfin tuna survived and made no overt locomotory changes when introduced directly into water

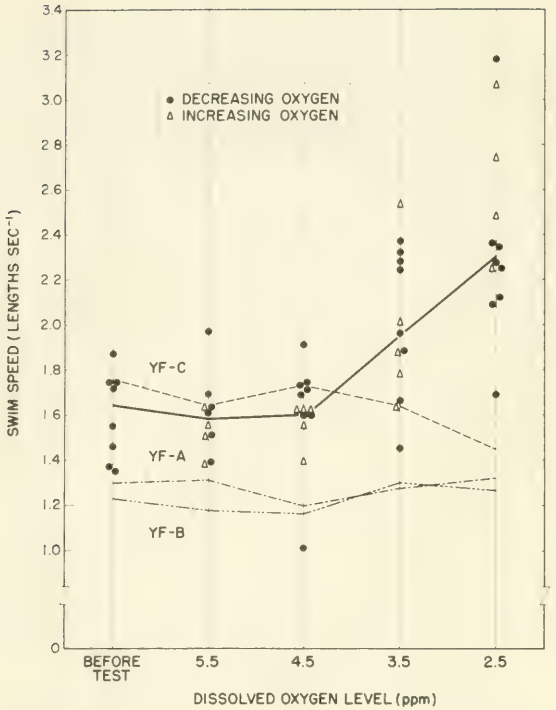

FIGURE 2.—Summary of data from the oxygen experiment observations from eight skipjack tuna and three yellowfin tuna. Dots — decreasing oxygen levels, median swim speeds grouped by 1-ppm intervals and "before" test observations. Open triangles — increasing oxygen levels, median swim speeds grouped by 1-ppm intervals. Solid line — grand median for eight skipjack tuna. Broken lines — medians for each of the three yellowfin tuna, decreasing oxygen levels only.

containing 1.4 and 1.6 ppm oxygen. They survived a 200-min exposure and a 100-min recovery period. By way of contrast, brook trout, *Salvelinus fontinalis*, LD_{50}'s for 1.5 ppm and 1.4 ppm were 300 and 100 min, respectively (Shepard 1955). The brook trout and the yellowfin tuna were swimming at about the same speeds, 1.0–1.5 lengths/s. Although conditions of the two experiments are in no way similar, these data do imply that yellowfin tuna are at least as low oxygen tolerant as brook trout. The higher energy requirements (larger fish, warmer water) of yellowfin tuna allow this conclusion. Perhaps if oxygen levels dropped low enough in my tank (1.4 ppm is about the lowest that could be achieved), an increase in speed similar to that in skipjack tuna would have been observed.

Increased swimming speed should function either to remove the fish from suboptimal areas (if coupled with some directive stimuli) or to provide more water to the gills—tunas are ram ventilators. Within the skipjack tuna habitat, water deficient in oxygen is found within and below the thermocline (Barkley et al. see footnote 1). Appropriate behavior would be to swim up and out of the low-oxygen water. Even without a change in direction, angle of attack of pectoral fins, or body attitude, increased swimming speed alone will cause a tuna to rise due to increased lift (Magnuson 1973).

Faster swimming speeds do not seem to be a response to increase ram ventilation (open mouth swimming). Increased flow over the gills providing more oxygen delivery is offset by increased respiratory demands imposed by faster swimming. Under conditions of saturated seawater (7.2 mg O_2/liter), 15% head loss along the respiratory flow path (Brown and Muir 1970), a conservative oxygen utilization factor of 75% (Stevens 1972), and a 1 cm^2 mouth gape (Brown and Muir 1970), oxygen is delivered to the gills at the rate represented by the middle broken line (Figure 3). This, of course, also increases as swimming speed increases. Respiratory demand (solid black line) and oxygen delivery intersect at two points: the lower is at the minimum swimming speed that can still furnish sufficient oxygen for an animal in an almost basal state and the upper is a point at which exponentially increasing respiratory demand again exceeds linearly increasing oxygen delivery.

The latter would seem to be maximum sustained swimming speed; anaerobic metabolism would be necessary at speeds above. However, neither function (anaerobic or aerobic) may be correctly extrapolated to the faster swimming speeds. Respiratory demand might well be less at higher speeds if swimming efficiency increases.

Yet, if dissolved oxygen concentration drops to 4 ppm, increase in swimming speed is an inefficient way to make up the deficit (lower broken line). But, increase gape to 2 cm^2 (I am assuming for argument's sake that this doubles ventilation volume) restores the amount of oxygen delivered (upper broken line). In summary, I suspect that increased swimming speed of skipjack tuna encountering oxygen-deficient water is not due to ram ventilation needs but rather is a behavioral response to remove an animal from a suboptimal area. Considering the relative expense of faster swimming in terms of oxygen needs, the modest increases in swimming speeds observed are probably very adaptive in that they should cause a

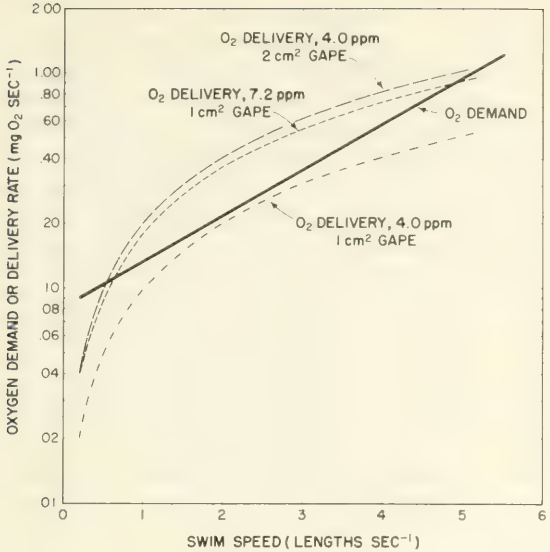

FIGURE 3.—Respiratory demand (Gooding and Neill see footnote 2) versus respiratory supply (Brown and Muir 1970; Stevens 1972) as a function of swimming speed in a 40-cm, 1.4-kg skipjack tuna. Respiratory demand increases geometrically while respiratory supply increases arithmetically with increasing swimming speed. When oxygen concentration decreases it is more efficient to increase ram ventilation by increasing gape rather than simply swimming faster.

fairly rapid rise in the water column at a relatively low energetic cost. Yellowfin tuna, in contrast, are just not stressed at the levels of saturation employed in our experiments. Yellowfin tuna should be able to occur in the anoxic water in or below the thermocline and since in the eastern central Pacific Ocean anoxic, cool waters are as inhospitable as the upper too warm waters, skipjack tuna may find no suitable habitat.

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A NONLETHAL LAVAGE DEVICE FOR SAMPLING STOMACH CONTENTS OF SMALL MARINE MAMMALS

Historically, the only expedient and successful method for determining the species upon which marine mammals feed has been to kill the animal, remove its stomach, and examine the contents in the laboratory (e.g., Wilke and Nicholson 1958; Tautsumi et al. 1961; Shomura and Hida 1965; Fiscus and Baines 1966; Fitch and Brownell 1968; Imler and Sarber 1947). This method, however, does not always work. For example, when actively feeding marine mammals are harpooned or shot, they sometimes regurgitate most or all of their food. While regurgitation by live captured marine mammals is possible, it does not appear to be a significant problem. Of the last 10 cetaceans that I have captured alive and later released unharmed, none has regurgitated during the capturing, handling, or releasing process. Although some researchers have reported on stomach samples from stranded marine mammals (e.g., Houck 1961; Fitch and Brownell 1968), these samples may not be representative of feeding habits of active healthy organisms.

Passage of the Marine Mammal Act in 1972 has made it necessary to develop techniques beside killing if we are to continue certain types of marine mammal research. A useful tool for determining feeding habits of delphinids and certain small pinnipeds would be a portable stomach pump device capable of being used in the field. To be effective, this device must be capable of removing small identifiable bits of food such as otoliths, scales, preopercular bones, squid beaks, or other

skeletal elements from the stomach of a pinniped, or forestomach of a small cetacean. I do not consider it essential to be able to remove whole fish or squid from marine mammal stomachs, as several recent or current marine mammal food habit studies have successfully utilized the above-mentioned skeletal elements for prey species identification (Fitch and Brownell 1968; Evans 1975; Burns and Lowry 1976).

Soft tissue digestion in pinnipeds and small cetaceans is normally quite rapid, thus it is possible to remove partially digested skeletal elements from the stomachs of live animals a few hours after the animal has eaten; and yet, because such elements as otoliths, preopercular bones, and squid beaks tend to resist this rapid digestion, they are still available for removal several hours after being consumed. In this paper I report on development and testing of a lavage designed to sample marine mammal stomach contents without killing the animal.

Methods

Several design criteria were considered essential. The lavage unit had to be effective in removing skeletal elements, simple to operate, portable, and capable of being used without injuring the animal. Discussions with persons who had pumped human stomachs or were familiar with the characteristics of marine mammal digestive tract anatomy resulted in the decision to utilize a water-driven aspirator to create suction. A 30-mm outside diameter by 1.0-m long Rousch Equine[1] endotracheal tube was modified for use as the irrigation and content removal device. These two pieces were coupled to a machined Plexiglas stomach content collection chamber with short sections of clear vinyl tubing. A ball valve was attached to the aspirator for vacuum control. The completed unit utilized normal city water pressure (35–50 psi) delivered through a 12-mm diameter rubber hose to the ball valve as driving source for the aspirator. A small hand pump was connected to the irrigation port on the side of the entubation tube so that warm (25°–35°C) water could be pumped into the animal's stomach to create a slurry which could be easily removed by light suction. To facilitate removal of this slurry, the entubation tube was modified by sealing the distal end (stomach end) with a machined Nylon plug, opening a side suction port (8.9 cm long by 1.25 cm wide) in the side of the tube 5 cm back from the Nylon plug, and removing the inflation cuff to allow passage of the irrigating solution into the stomach opposite the suction port. The assembled unit is detailed in Figures 1 and 2. The completed unit was tested in the laboratory using a 2-liter beaker in place of a marine mammal stomach.

Marine mammals were first tested at the Naval Undersea Center and Sea World, Inc. in San Diego, Calif., in December 1975. A total of five animals were lavaged, including two California sea lions, *Zalophus californianus,* two Pacific white sided porpoise, *Langenorhynchus obliquidens,* and one bottlenose porpoise, *Tursiops truncatus.* Animal weights ranged from 70 kg for the smallest *Z. californianus* to 210 kg for the *T. truncatus.* All animals except a 100-kg *Z. californianus* had fasted for at least 24 h prior to being lavaged. The

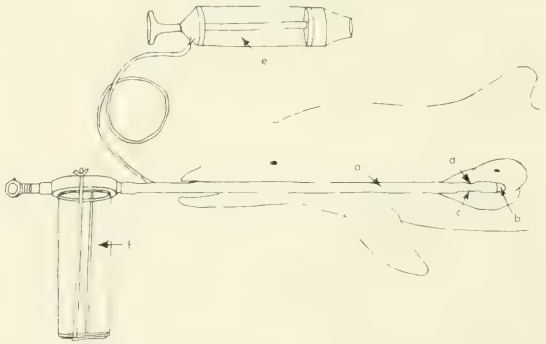

FIGURE 1.—Schematic of lavage device. Entubation tube (a), Nylon end plug (b), side suction port (c), irrigation port (d), irrigating solution hand pump (e), stomach content collection chamber (f).

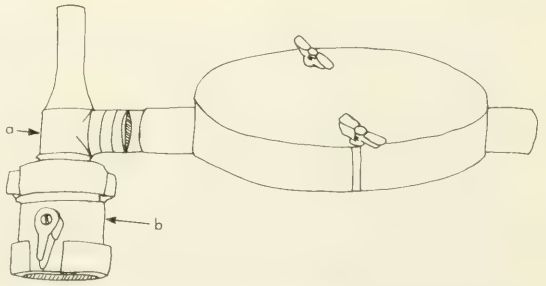

FIGURE 2.—Oblique view of the aspirator (a) and control valve (b) attached to the top of the collecting chamber of lavage device.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

100-kg sea lion had been fed 5 kg of surf smelt, *Hypomesus pretiosus*, 3 h prior to being lavaged.

Successful lavage required two procedures: 1) restraint of the animal and 2) entubation, irrigation, and suction. Restraint varied greatly depending on whether a pinniped or cetacean was to be lavaged. Delphinids are generally easy to restrain. The procedure many investigators have used with success utilizes a canvas sling and U-shaped pipe frame to hold the animal (Ridgway 1972). Normally the use of a sling is sufficient restraint, however A. B. Irvine (pers. commun.) has also used a wooden step ladder covered with closed cell foam padding and padded straps to restrain large or especially aggressive delphinids. This latter procedure requires that the animal be gently lowered onto the padded ladder and then immobilized with the padded straps. Pinnipeds are more difficult to restrain in the field than delphinids. Squeeze cages (Ridgway 1972) are generally effective, but are normally too cumbersome and heavy to use at sea. During the lavage test in San Diego, the squeeze cage was used with success, though considerable care was taken to avoid being severely bitten. Use of the padded wooden ladder and straps as a restraining technique for pinnipeds in the field appears reasonable but needs testing.

With the animal successfully restrained, we proceeded with entubation after lubricating the entubation tube with a jelly lubricant. The plugged end of the tube was gently pushed down the animal's esophagus. After completing the entubation I waited a few moments to make sure the animal was breathing normally. If the animal gagged or abnormal respiration was evident, I quickly but gently removed the tube. If respiration was normal, I connected the content collection chamber and irrigation solution hose and pumped about 300 ml of warm water into the stomach. Warm water was used to avoid thermal shock to the stomach. I then opened the vacuum control valve and applied suction to the stomach. As suction began to remove the stomach content slurry, more irrigating solution was pumped into the stomach. In this manner a 2- to 3-liter food sample was collected in a period of about 5 min. When I felt I had collected sufficient material for test purposes, I shut off the suction, ceased pumping irrigating solution, and gently removed the stomach tube. The stomach contents were filtered from the slurry using a small hand vacuum pump and then preserved in 70% alcohol.

Results

Using the above procedure otoliths, muscle myomeres, skeletal bones, and scales were collected from all five marine mammals. The animals tested were returned to their tanks unharmed and were doing well several days later.

Discussion

Using the equipment described and associated procedure it was possible to remove almost all of the diluted stomach slurry by suction; and by rotating the tube while suctioning, it was possible to vacuum the rugae of the stomach in order to collect otoliths and squid beaks which tend to accumulate in these folds. J. E. Fitch of the California Department of Fish and Game has used fish otoliths as a means to identify prey species on a routine basis. With experience it is possible to correlate size of otoliths and approximate sizes and weights of the intact fish. The Alaska Department of Fish and Game is presently establishing such an otolith reference collection, allowing not only identification of otoliths but also estimation of intact prey length and weight (L. F. Lowry pers. commun.).

The limiting factor in the use of this device appears to be the ability of the capture personnel to restrain specimens. Pinnipeds over 150 kg are probably too large to be effectively restrained mechanically, and are therefore very difficult or impossible to entubate. Cetaceans, perhaps as large as 500 kg, can be effectively entubated and lavaged since these animals are generally much more easily restrained out of water than the pinnipedia. In addition, certain pinnipeds, e.g., *Erignathus barbatus, Phoca hispida, P. fasciata,* feed to a greater or lesser degree on soft-bodied crustaceans, and these prey organisms would probably be effectively destroyed by suction and passage through the entubation tube (L. F. Lowry pers. commun.).

I have made no mention of the use of chemorestraining techniques because I feel that these methods are still unsuited for general use in the field, especially with cetaceans. With proper supervision, they have proven effective for restraining captive pinnipeds. In August 1972, I used a chemorestraining solution of Ketamine–Atropine on *Z. californianus* in the field. Although dosages were at the level recommended by marine mammal research veterinarians, I found the drugs

to be too slow acting to be generally effective for stopping highly mobile pinniped species before they could reach the sea. Two major drawbacks to chemorestraints in a field situation are judging animals' size adequately for effective dose determination, and the time required for the animal to recover sufficiently to be able to swim unassisted and maintain pace with the herd or pod from which it was captured. Should future work develop either drugs or techniques which allow safe and semi-instantaneous chemorestraint of any marine mammal species, then these drugs or techniques would be extremely useful when used in connection with the stomach pump. Until such drugs are available, I believe physical restraint is indicated during the lavage procedure.

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I am indebted to S. H. Ridgway and the personnel at the Naval Undersea Center for their patience and cooperation, and to Lanny Cornell and his staff at Sea World, Inc. for their cooperation during testing of this lavage device. I thank L. F. Lowry of the Alaska Department of Fish and Game and A. B. Irvine of the U.S. Fish and Wildlife Service for their comments concerning restraint and use of this technique. I also thank Larry Hobbs and Mike Honing of University of California Santa Cruz and Steve Leatherwood of the Naval Undersea Center for assisting me during tests of the lavage. Thanks also to S. B. Stone of Marine General Hospital, K. S. Norris, T. P. Dohl, and R. W. Pierce of University of California Santa Cruz for their comments concerning design of the equipment. K. S. Norris, J. S. Leatherwood, W. E. Evans, T. P. Dohl, and Robert Hoffman reviewed the manuscript. This work was supported by contract number MM4AC013 from the U.S. Marine Mammal Commission.

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LIFE HISTORY, FEEDING HABITS, AND FUNCTIONAL MORPHOLOGY OF JUVENILE SCIAENID FISHES IN THE YORK RIVER ESTUARY, VIRGINIA[1,2]

LABBISH N. CHAO[3] AND JOHN A. MUSICK[4]

ABSTRACT

Four abundant sciaenid fishes, *Cynoscion regalis, Bairdiella chrysoura, Micropogonias undulatus,* and *Leiostomus xanthurus,* use the York River, Va., as a nursery ground and as an adult seasonal feeding ground. In addition, six species of sciaenids, *Menticirrhus saxatilis, M. americanus, Sciaenops ocellata, Cynoscion nebulosus, Pogonias cromis,* and *Larimus fasciatus,* are present in the estuary occasionally. Yearling *C. regalis* were first caught in April and young-of-the-year in July or August. Yearling *B. chrysoura* were first caught in March or April and young-of-the-year in July or August. Juvenile *Micropogonias undulatus* and *Leiostomus xanthurus* may be present in the York River all year-round. Young-of-the-year *L. xanthurus* were first caught in April and *M. undulatus* were first caught in August. Small *M. undulatus* (<20 mm TL) were caught from August to June, which may indicate a prolonged spawning season (or a late spawning stock). Emigration to the ocean was found in all the four species during late fall or early winter. Water temperature and dissolved oxygen seemed to be the most important factors in the spatial and temporal distributions of these four species in the York River.

Mouth position, dentition, gill rakers, digestive tract, pores and barbels, nares, and body shape of six sciaenid species, *Larimus fasciatus, C. regalis, B. chrysoura, M. undulatus, Menticirrhus saxatilis,* and *Leiostomus xanthurus,* were found to be important in locating and ingesting prey in the water column. Stomach contents indicated that the food partitioning of these six species was closely correlated with the species and their prey habitat. *Larimus fasciatus, C. regalis,* and *B. chrysoura* fed mainly above the bottom, whereas *Micropogonias undulatus, Menticirrhus saxatilis,* and *L. xanthurus* fed on epifauna, infauna, or both. Juvenile sciaenids are able to coexist in the same area because of differences in spatial and temporal distribution, relative abundance, and food habits.

Sciaenid fishes are among the most important inshore bottom fishery resources of the Atlantic and Gulf of Mexico coasts of the United States (Roithmayr 1965; Joseph 1972; Gutherz et al. 1975). Sciaenid fishes usually use the estuary as a nursery ground and seasonal feeding ground. Among the 14 species of sciaenids recorded from Chesapeake Bay proper (Musick 1972), young-of-the-year of 10 species were caught in the York River system during this study. *Leiostomus xanthurus, Micropogonias undulatus, Bairdiella chrysoura,* and *Cynoscion regalis* were the most abundant species. *Menticirrhus saxatilis, M. americanus, Sciaenops ocellata, C. nebulosus, Pogonias cromis,* and *Larimus fasciatus* were caught only occasionally.

Juvenile sciaenids, except the Atlantic croaker, *Micropogonias undulatus*, usually entered the York River in late spring and left in late fall. During this period, sciaenid fishes dominated bottom trawl catches in the York River (Colvocoresses 1975; Markle 1976). By yearly average, they composed more than 50% of the total catch by weight and 18 to 28% by number of individuals. The purpose of this study is to describe the coexistence of the four most abundant juvenile sciaenids in the York River system, Va., based upon relative abundance, temporal and spatial distribution, length frequency, apparent movements, and feeding habits. Morphological structures related to feeding habits and habitats were also studied. Specimens of the banded drum, *Larimus fasciatus,* and the northern kingfish, *Menticirrhus saxatilis*, were included to show the range of variability in the feeding habits of juvenile sciaenids. Bottom trawl surveys conducted by the Virginia Institute of Marine Science (VIMS) from January 1972 to

[1]A portion of a dissertation submitted to the School of Marine Science, College of William and Mary, Williamsburg, Va., in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Marine Science, by the first author, May 1976.

[2]Contribution No. 816, Virginia Institute of Marine Science, Gloucester Point, Va.

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December 1974 provided the data for analyses of distribution and food habits. An analysis of fish community structure based on this data has been reported by Colvocoresses (1975).

The York River and its major tributaries (Pamunkey and Mattaponi rivers) represent an estuarine system which is relatively well known biologically and is relatively undisturbed (Boesch 1971). The general trend of geomorphology, hydrography (salinity, dissolved oxygen, and temperature), ecology, and alteration by man of the area were described by McHugh (1967), Boesch (1971), and Brehmer.[5]

MATERIALS AND METHODS

Survey Programs

Seven longitudinal strata (A, B, C, D, E, F, and G) and three cross-sectional substrata (north shoal, channel, and south shoal) within each stratum were sampled monthly (Figure 1). Shoal hauls were usually in water <4 m and channel hauls in water >5 m deep. Randomly numbered square grids (540 m on a side) were assigned as trawl stations. In the lower 16 km (10 miles) of the York River, strata A, B, C, and D were sampled from March 1972 to December 1974. The upper part of the York River was sampled from January 1972 to March 1974, but the random method was not used until June 1972 and strata E, F, and G were not designated until January 1973. Before the random sampling program, fixed sampling stations in the channel were assigned at 8-km (5-mi) intervals from the mouth of the York River (mile zero) up to 45 km (mile 28, also see Haven 1957; Markle 1976). Data from fixed station samples (January–May 1972) were combined within the strata for analyses. Lower portions of the Mattaponi and Pamunkey rivers (strata: M and P) were sampled after January 1973. Three substrata (1, 2, and 3) were set at 8-km (5-mi) intervals for the lower 24 km (15 mi) upstream from their confluence with the York River (about 45 km from the York River mouth). Each sampling stratum was divided into station grids, each measuring 540 m on a side; four to six grid stations were sampled randomly from each stratum monthly.

Gear

Bottom trawl tows were against the current, of 5-min duration on the bottom with a 4.9-m (16-ft) semiballoon otter trawl (7-m rope, 1.9-cm bar mesh, 0.63-cm bar mesh cod end liner), 7-m bridle, and 0.6-m weighted otter doors at a speed of approximately 90 m/min. Nine stations were sampled monthly with beach seines along the shores of lower parts (strata A–D) of the York River (Figure 1) and three replicate hauls were made with a 15.25-m (50-ft) bag seine (1.8 m deep with a square bag, 0.64-cm bar mesh in the wing and 0.48-cm bar mesh in the bag). Thirteen beach seine stations were selected along the shores of the upper part of the York River (strata E–G, Figure 1). These stations were only sampled from July to October in 1972 and 1973 with a 30.5-m (100-ft) bag seine. Beach seine data were used only for length frequency analysis in the present study. Hydrographic (salinity, temperature, and dissolved oxygen) data were collected from both surface and bottom water.

Sampling Procedure

All fishes were identified, counted, and weighed in the field or laboratory. Total length (TL), measured from snout to the posterior tip of the caudal fin (on the midline), was taken to the nearest millimeter. All individuals of each species were measured from each trawl haul. For very large catches, at least 25 individuals were subsampled. Specimens were randomly selected for stomach analyses and preserved in 10% Formalin;[6] stomachs were dissected out and transferred to 40% isopropanol or 70% ethanol. Stomach contents were identified to the lowest practical taxon and frequency of occurrence of each item was recorded.

The standard methods of Hubbs and Lagler (1964) were used for all counts and measurements, if applicable. Upper and lower jaw lengths were measured from tips of the premaxilla and dentary, respectively, to the symphysis at the posterior corner of the mouth gape. Digestive tracts were removed from the fish. The intestine was straightened and measured from its junction with the stomach to the anus. Osteological observations

[5]Brehmer, M. L. 1970. Biological and chemical studies of Virginia's estuaries. Unpubl. manuscr., 120 p. Va. Inst. Mar. Sci., Gloucester Point.

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

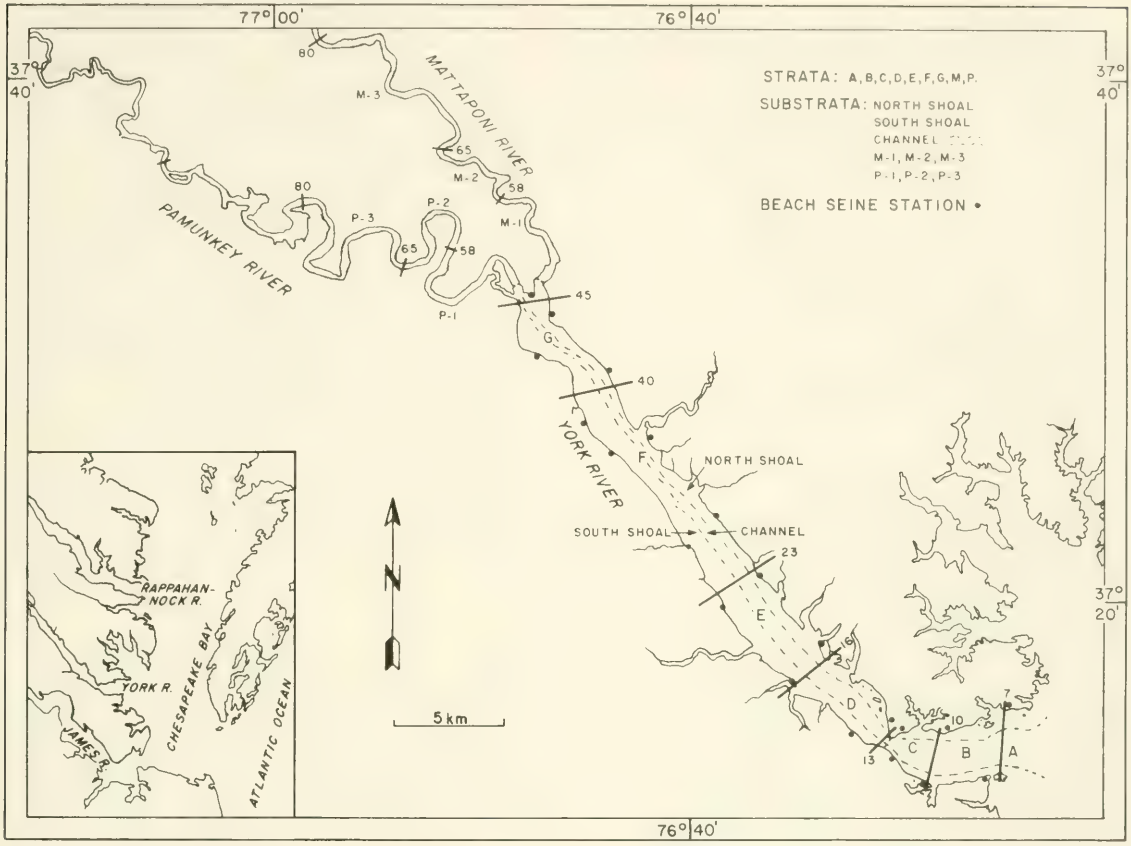


FIGURE 1.—The trawl strata, substrata, and beach seine stations in the York River estuary, Va. Strata: A–G, M, and P. Substrata: north shoal, channel, and south shoal. Substrata in Mattaponi River expressed as M-1, M-2, and M-3, in Pamunkey River as P-1, P-2, and P-3. River distances from the mouth of York River (0 km) are indicated in kilometers.

were made on cleared and stained specimens, according to the methodology of Taylor (1967).

The nomenclature used for the study fishes follows Chao (in press). *Micropogonias* must replace *Micropogon* because the generic name *Micropogon* was preoccupied by Boie (1826 in Aves). The specific name *chrysoura* is used instead of *chrysura* for *Bairdiella* because the spelling *chrysourus* was used by the original author (Lacepède 1803:166).

RESULTS AND DISCUSSION

Hydrographic Description

Water depth, temperature, salinity, and dissolved oxygen were measured with each sample and are listed in the appendix section of Chao (1976). The benthic environment was of particular importance to the present study. Mean values for bottom temperature, salinity, and dissolved oxygen in each stratum from May 1972 to August 1973 are summarized in Figure 2, to show seasonal patterns in the York River estuary.

Temperature

The bottom water temperature of the York River (Figure 2) was lowest in January and highest in July (1973) or August (1972). The gradual increase of temperature from April to June and the decrease from October to December are most important to migratory fishes in the York River (Markle 1976). In winter months (December–February), the bottom temperature of the upper portion of the York River was lower than that of the lower portion. No apparent differences in temperature were found among the shoal and the

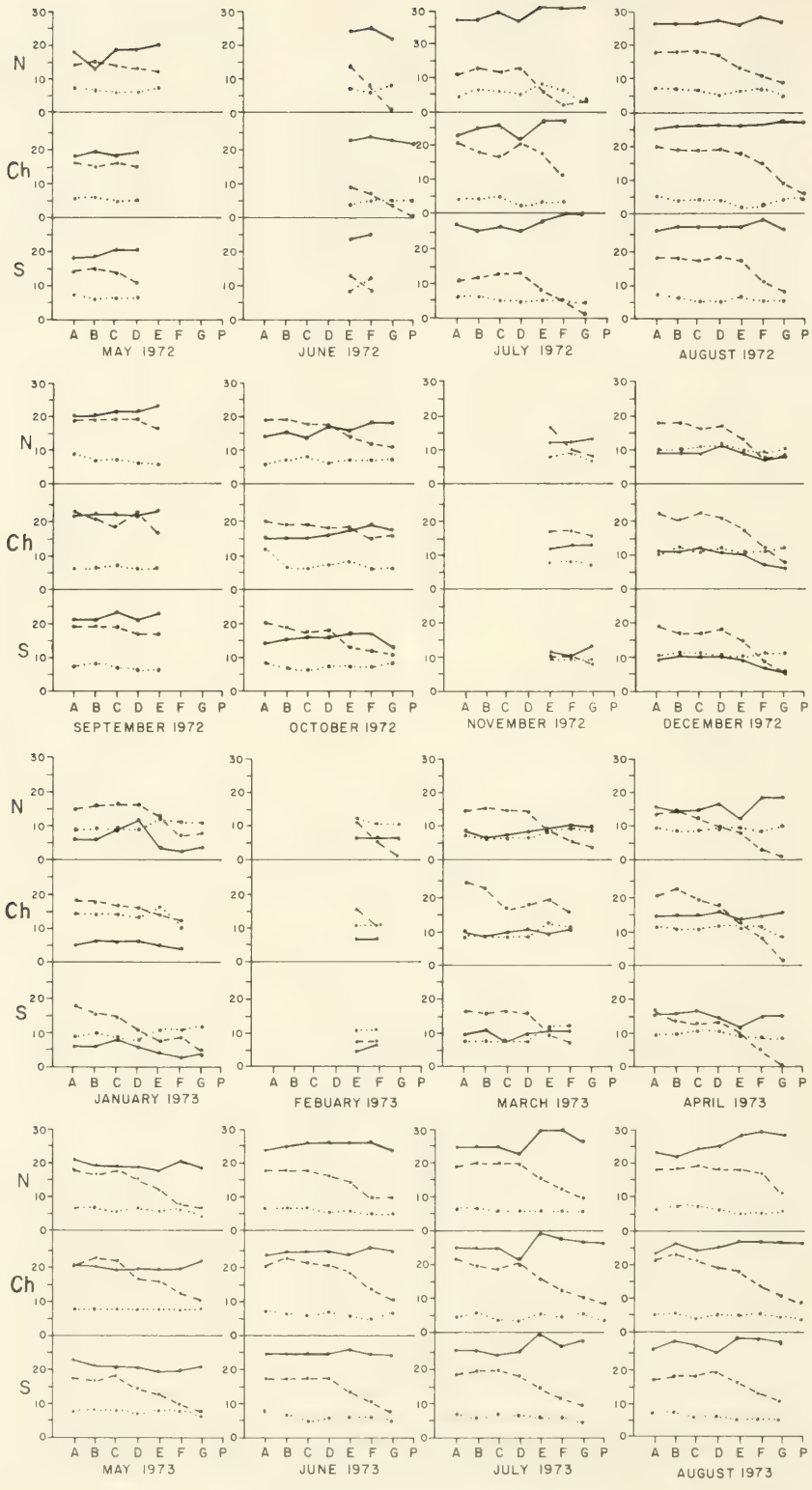


FIGURE 2.—Monthly means of the bottom temperature (℃—solid line), salinity (‰—dashed line), and dissolved oxygen (milligrams/liter—dotted line) in the York River estuary from May 1972 to August 1973. Strata: A–G in York River and P in Pamunkey River. Substrata: N = north shoal, Ch = channel and S = south shoal.

channel stations. In spring months (March–May), bottom temperatures increased rapidly, and the upper portion of the York River had slightly higher temperatures than the lower portion. The shoal stations also showed a slightly higher mean bottom temperature than the channel stations. In summer months (June–August), the bottom temperature of the upper portion of the river was higher than the lower portion. The shoal stations also showed a higher mean bottom temperature than the channel stations. In fall months (September–November), bottom temperature decreased rapidly. The upper portion of the river had slightly higher temperatures than the lower portion in the early fall (September–October). In early winter (December), bottom water temperature was slightly higher in the lower portion of the river (Figure 2). No apparent differences were found among the shoal and channel stations.

Dissolved Oxygen

Dissolved oxygen in the York River (Figure 2) was generally lower in warmer months (May–October) and higher in colder months (November–April). In the warmer months, dissolved oxygen was lowest at the deeper channel stations. There was no apparent difference between the upper and lower portions of the York River. In colder months, dissolved oxygen was slightly higher in the upper portion of the river and no apparent difference was found among shoal and channel stations.

Salinity

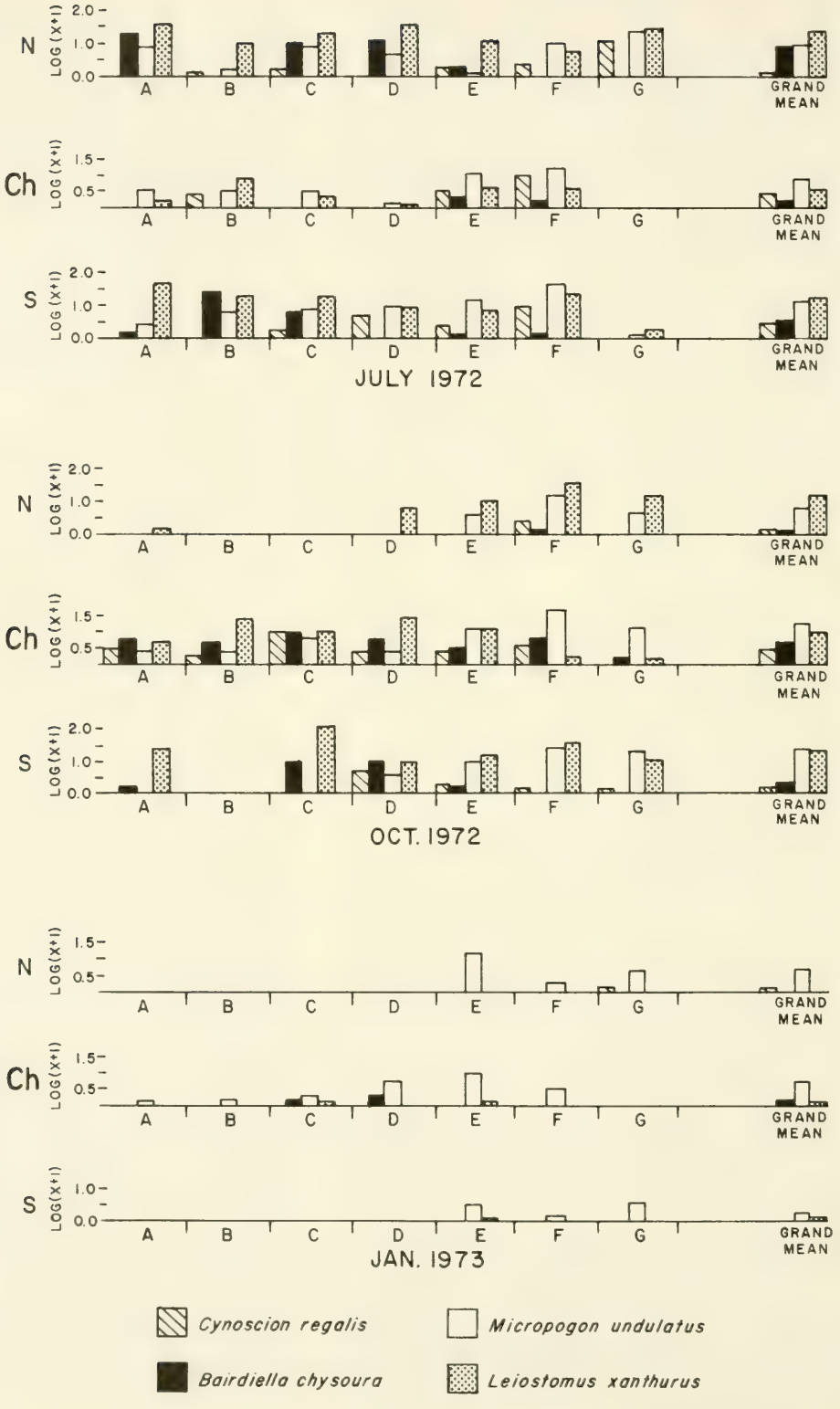
Salinity decreased toward the upper portion of the York River (Figure 2). Lower salinities usually were found in spring (March–May) and winter (December–February). The extremely low salinities of June to August 1972, were caused by hurricane Agnes (Anderson et al. 1973). Salinity at channel stations was usually higher than at shoal stations, especially in the lower portion of the river from March to June.

Temporal and Spatial Distributions

Young sciaenids are among the most abundant migratory finfishes in the York River (Massmann 1962; Colvocoresses 1975; Markle 1976). Temporal and spatial distributions of juveniles of the four most abundant sciaenids, *Cynoscion regalis*, *Bairdiella chrysoura*, *Micropogonias undulatus*, and *Leiostomus xanthurus*, are compared (Figures 3–5) to determine ecological partitioning during their estuarine life. The relative abundance of each species is expressed by the geometric mean, $\log_{10}(x + 1)$, of the individual catches per tow within the substrata, where x is the mean number of individuals per tow. Four months (July, October, January, and April) were selected to represent the seasonal abundances from different parts of the York River (Figure 3). Monthly mean catches per tow by river distance (stratum) and depth (substratum) were compared (Figures 3–5). Fishes caught in the Mattaponi and Pamunkey rivers were compared only by river distance (Figure 4).

In July 1972 and 1973, all four species of juvenile sciaenids were present in all parts of the estuary except the upper part (Figures 3–5). Relative abundance varied among species (Figure 3). *Bairdiella chrysoura* was more abundant in the lower and middle part of the river, while *C. regalis* and *M. undulatus* were more abundant in the upper part of the river (Figure 5). *Leiostomus xanthurus* was ubiquitous. *Micropogonias undulatus* gradually declined in abundance upstream in both the Mattaponi and Paumkey rivers (Figures 4, 5). *Leiostomus xanthurus* catches were quite variable in the Pamunkey River. This may have been caused by the contagious distribution of this species. Sciaenids were more abundant in shoal stations (Figure 3) than channel stations, especially in July 1972. Colvocoresses (1975) and Markle (1976) noted a general decline in the mean number of species and individuals of fishes caught per month in the summer from channel stations. This may be attributed to a reduction in the dissolved oxygen concentration, usually below 5 mg/l at the bottom of the channel (Markle 1976; Brehmer see footnote 5), and was apparently the case in the present study (Figure 2). Catches of *C. regalis* did not decline in channel stations, but this species is the best adapted for pelagic life of the four species studied (see "Correlation of Feeding Structures and Food Habits" section), and may have been captured in midwater where dissolved oxygen values did not decline.

In October (1972, 1973) juveniles of all four species of sciaenids were present in all parts of the estuary (Figure 3) and all reached their highest total abundance (Markle 1976). *Cynoscion regalis* was more abundant in the lower parts of the York River; *B. chrysoura* and *L. xanthurus* were more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GRAND MEAN
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Micropogon undulatus
Bairdiella chysoura
Leiostomus xanthurus

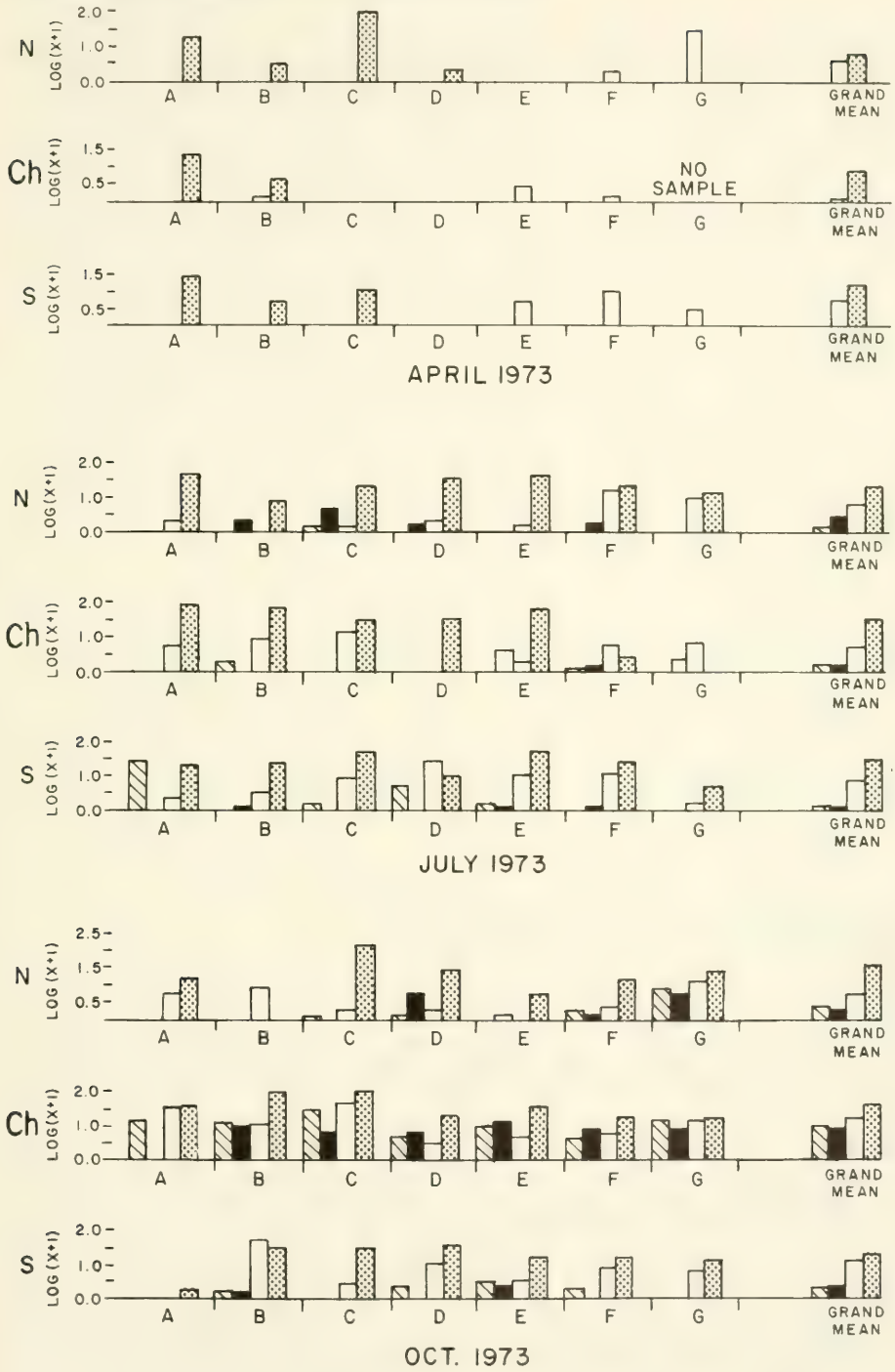


FIGURE 3.—Seasonal abundance of four juvenile sciaenids with depth and distance upstream in the York River. Mean numerical catch per tow of each substratum expressed as log $(x + 1)$. Strata: A–G; substrata: N = north shoal, Ch = channel, and S = south shoal.

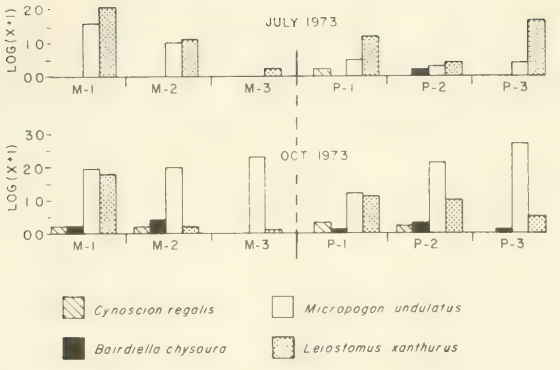


FIGURE 4.—Seasonal abundance of four juvenile sciaenids in the Mattaponi and Pamunkey rivers. Mean numerical catch per tow of each substratum expressed as log $(x + 1)$. Strata: M = Mattaponi River, P = Pamunkey River. Substrata: 1, 2, and 3 designated by river distance upstream.

abundant in the middle part of the river. *Micropogonias undulatus* was more abundant in the upper part of the river, and especially in the Mattaponi and Pamunkey rivers (Figures 4, 5). Mean catch per tow increased up the estuary. Depth distribution of these four species of sciaenids indicated that they were more abundant in the channel stations (Figure 3). The relative abundance at south shoal stations was higher than at north shoal stations. The area was larger and the sampling depth was greater in the south shoal than the north shoal area (Colvocresses 1975; Chao 1976). Also, the average size of young sciaenids, especially the young-of-the-year groups, was larger in the channel than in the shoal stations (see section on "Distribution and Size"). Larger size juvenile sciaenids might use deeper areas to seek food and shelter.

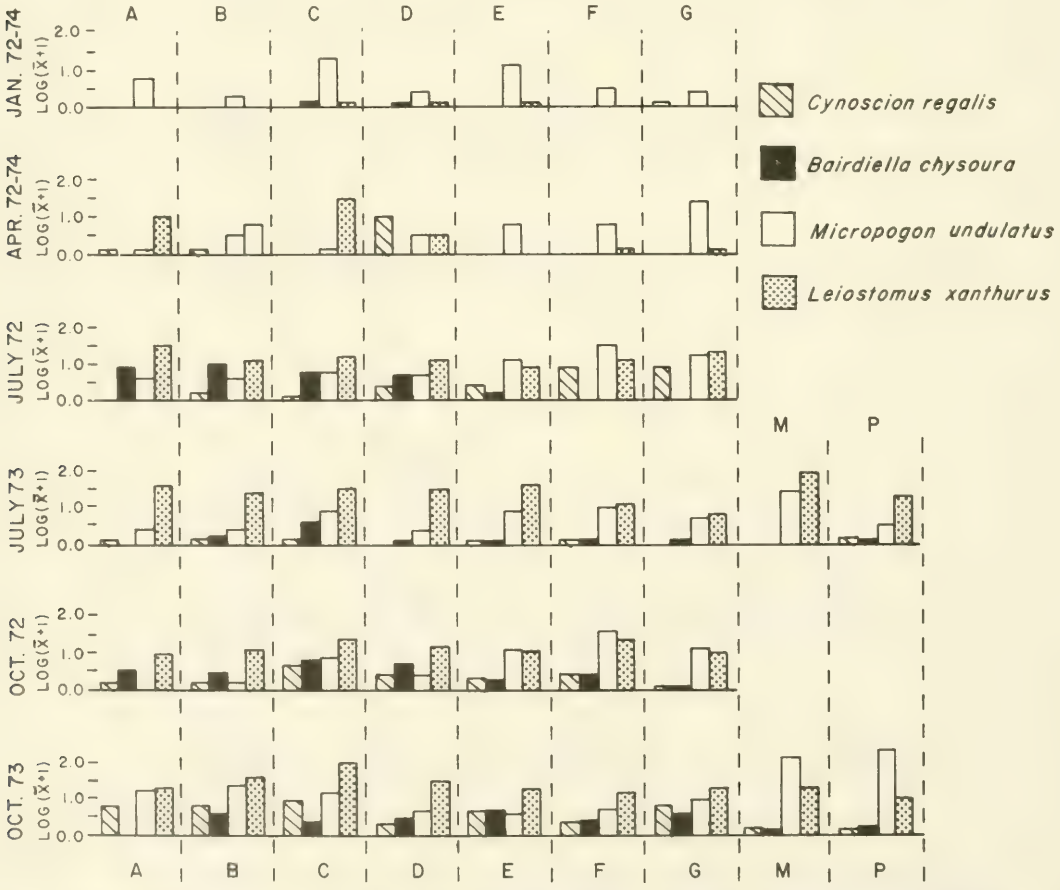


FIGURE 5.—Seasonal mean abundance of four juvenile sciaenids along the salinity gradient (strata) in the York River estuary. Grand mean numerical catch of four juvenile sciaenids per tow of stratum expressed as log $(x + 1)$. Strata: A–G in York River, M = Mattaponi River, P = Pamunkey River. Grand means of January and April represent the average of 3 yr. (1972 to 1974).

In January 1972–74, the numbers of individual sciaenid fishes were considerably reduced, except for *M. undulatus* (Figures 3, 5). *Cynoscion regalis, B. chrysoura,* and *L. xanthurus* were caught only occasionally. During the winter months, resident fish species were more abundant than transients, especially in the upper tributaries of the York River (Markle 1976). *Micropogonias undulatus* was the most abundant sciaenid fish in the middle part of the York River (Figure 5). Depth distribution in January 1973 (Figure 3), indicated that most fish were caught in the channel. Bottom temperatures of the channel stations were higher than shoal stations (Figure 2), which might have been the major factor causing the concentration of young sciaenids in the channel.

In April 1972–74, *C. regalis, M. undulatus,* and *L. xanthurus* were caught (Figures 3, 5). *Cynoscion regalis* was absent in 1973 (Figure 3) but sparse in 1972 and 1974 (Figure 5). *Micropogonias undulatus* was more abundant in the upper part of the river and *L. xanthurus* was more abundant in the lower reaches (Figures 4, 5), apparently because the young-of-the-year *L. xanthurus* had just entered the estuary (see section on "Distribution and Size"). Depth distribution of these two species (Figure 3) showed that they were more abundant in shoal areas, especially *M. undulatus*. *Bairdiella chrysoura* was completely absent.

Life History and Size

Length-frequency distributions (Figures 6–19) indicate that juvenile *Leiostomus xanthurus, Bairdiella chrysoura, Cynoscion regalis,* and *Micropogonias undulatus* enter the York River consecutively from April on, and all but *M. undulatus* leave the York River by December. Seasonal size distributions of these four species in the York River will be discussed individually and compared with studies from other areas. Modes I and II in Figures 6 and 10 and the following discussions represent young-of-the-year (mode I) and yearlings (or older fishes, mode II), respectively, except in *M. undulatus* and Figure 16, where modes I and II represent young-of-the-year and mode III the yearlings (or older fishes).

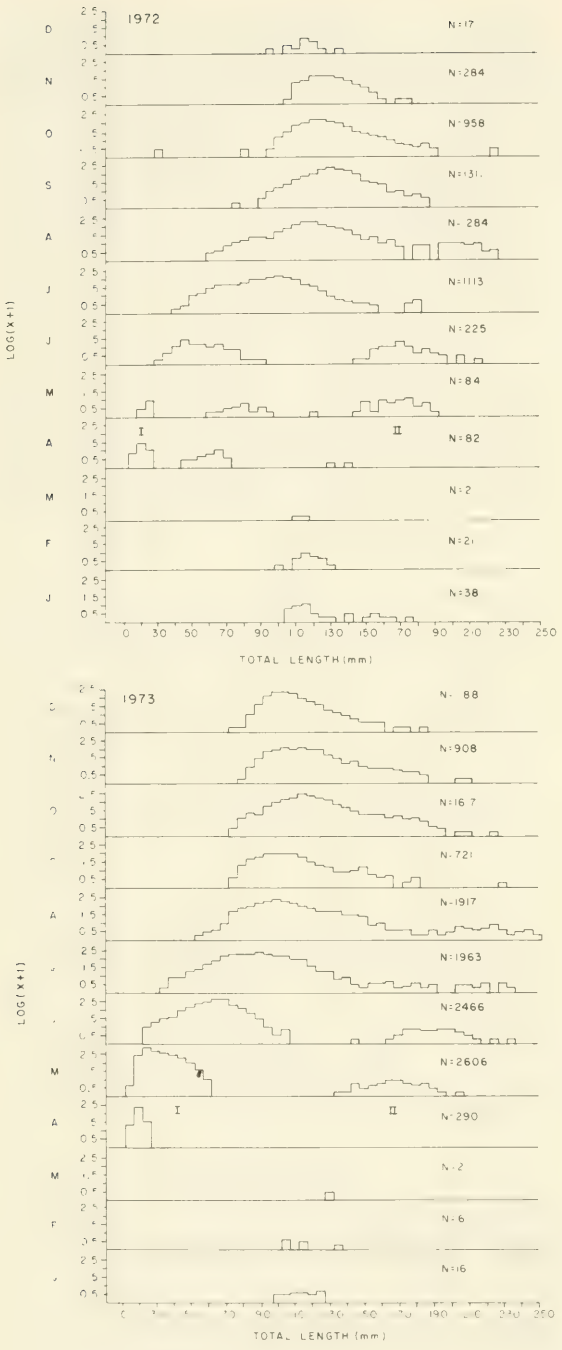
Leiostomus xanthurus Lacepède—Spot

EARLY LIFE HISTORY IN THE YORK RIVER.—Young-of-the-year spot, entered the trawl and beach seine catches in early April and most left by December (Figure 6, mode I). A few smaller fish stayed in the estuary over winter. Yearling spot usually entered the study area from March to May and left the area in September (Figure 6, mode II). The intermediate mode (between modes I and II) on Figure 6, April and May 1972, was not found in the 1973 and 1974 samples. This may indicate late spawning in the previous year (1971). The length frequencies of young spot from May to July during 1972–74 were pooled and grouped by river strata (Figure 7). Young-of-the-year spot moved up to the confluence of the Pamunkey and Mattaponi rivers (Figure 1); most yearling spot stayed in the lower parts of the York River. During the same periods, no differences were found between the length frequency distributions in shoal and channel stations (Figure 8) of either young-of-the-year or yearling spot.

Spot caught in the beach seine (Figure 8) were obviously smaller than those taken by trawls. Spot was the most abundant sciaenid in the beach seine zone (depth <1.5 m) for collections with the 15.25-m and 30.5-m seines. The length frequency distribution of spot caught by beach seine was typically unimodal; mostly young-of-the-year (Figure 9). Some smaller yearlings were taken occasionally (Figure 9, 1974, mode II) and individuals >135 mm TL were captured only with the 30.5-m seine (Figure 9, August and September 1972).

In summary, young-of-the-year spot entered the York River in April and used the estuary as a nursery ground. In December, most spot left though some smaller fish stayed in the estuary through the winter, joining the yearlings as they returned to the river in the next spring. The yearlings left the estuary after an extended feeding period from March to October.

OTHER STUDIES.—Selected length frequency data for spot along the Atlantic and Gulf of Mexico coasts of the United States are summarized (Table 1) for comparison with the present study. Hildebrand and Schroeder (1928) and Pacheco (1957, 1962a) reported length frequency of spot from the present study area (York River and Chesapeake Bay). Across all areas (Table 1), young-of-the-year spot (Group 0 on Table 1) enter the estuarine nursery grounds during the first half of the year. They may enter estuaries as early as January (Table 1; Hildebrand and Cable 1930; Springer and Woodburn 1960; Sundararaj 1960). Spot first enter the



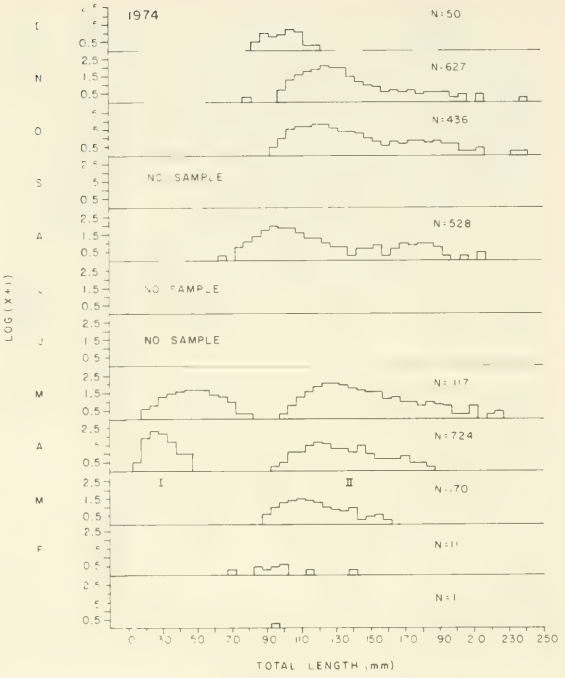


FIGURE 6.—Monthly length-frequency distributions of juvenile spot, *Leiostomus xanthurus*, from York River, 1972–74. Mode I, young-of-the-year; mode II, yearlings. Frequencies expressed as log $(x + 1)$ at 5-mm increments. Only the lower portion of river (strata A–D) is represented in 1974.

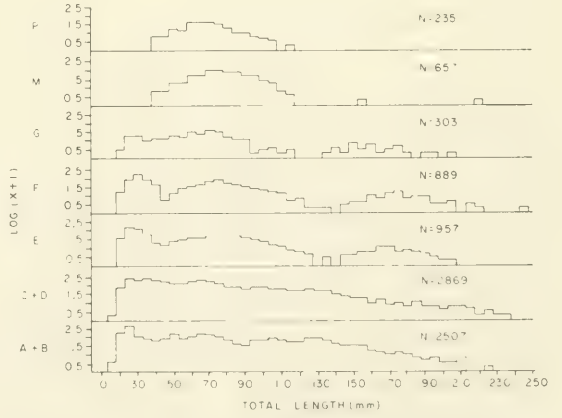


FIGURE 7.—Length-frequency distributions of spot, *Leiostomus xanthurus*, by river distance (strata) upstream in the York River estuary. Pooled total, May to July 1972–74. Strata: A–G in York River, M = Mattaponi River, P = Pamunkey River. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

estuary in February along the Atlantic coast of Georgia (Music 1974) and the Gulf of Mexico coast of Florida (Townsend 1956), Louisiana (Dunham 1972), and Texas (Parker 1971). In South Carolina (Dawson 1958; Shealy et al. 1974), North Carolina (Hildebrand and Cable 1930), and the lower Chesapeake Bay (Hildebrand and Schroeder 1928

TABLE 1.—Growth of spot, *Leiostomus xanthurus*, from different estuarine areas along U.S. Atlantic and Gulf of Mexico coasts.

Author	Thomas 1971		Young 1953		Hildebrand and Schroeder 1928		Pacheco 1957		Chao 1976	
Locality	Delaware River, Del.		Chesapeake Bay, Md.		Chesapeake Bay		Lower Chesapeake Bay and York River, Va		York River, Va.	
Period	June 1968–Sept. 1970		May–Oct. 1951		Prior to 1928		May 1955–Feb. 1956		Jan. 1972–Dec. 1974	
Gear[1]	16-ft T and S		75 x 4 ft Haul S.		?		P and 30-ft T		16-ft T and S	
Source	Table 68		Tables 4 and 5		Table on p. 273		Table 3		Fig. 6 (present study)	
Length (mm)	Total length		Total length		Total length		Total length		Total length	
Age-group[2]	0	I	0		0	I	0	I	0	I
January						75-149		155-255		95-175
February								150-275		70-140
March					15-19					90-160
April					20-24				15-65	95-185
May			16-60		15-74	155-174	80-105	130-225	20-95	95-225
June	19.2		26-80		20-99	115-174	115-(140)	(145)-210	25-105	140-235
July	30- 80	90-140	(26-130)		40-124	135-209	115-(150)	(155)-230	35-155	155-235
August	45-100	110-165	86-90		65-149		125-(180)	(200)-245	55-(175)	(160)-250
September		120-170	86-106		94-170	190-209	135-(185)	(190)-260	70-185	230
October		125-175	(71-155)		100-184	190-299	135-(235)		80-(195)	(170)-240
November					75-184		165-(205)		80-185	(160)-240
December					75-119		155-185	220-240	75-190	

Author	Hildebrand and Cable 1930		Shealy et al. 1974		Music 1974		Townsend 1956		Springer and Woodburn 1960	
Locality	Beaufort, N.C.		South Carolina		Georgia		Alligator Harbor, Fla.		Tampa Bay, Fla	
Period	Prior to 1930		Feb. 1973–Jan. 1974		Oct. 1970–Sept. 1973		Mar. 1955–May 1956		Jan.–Dec. 1958	
Gear[1]	PI and T		20-ft T		40-ft T, 12-ft S, 300-ft G		150- and 600-ft S		T, 80-ft S, and Pu	
Source	Tables 7 and 8		Table 27		Fig. 10		Table I		Table 13	
Length (mm)	Total length		Total length		Total length		Total length		Standard length	
Age-group[2]	0	1	0	1	0	1	0	1	0	
January	4-21	82-195		88-207		80-250			13-31	
February	3-27	91-200		83-142	10-35	85-225	10-34	95-159	13-49	
March	10-39	93-200		113-182	10-40	95-225	15-54	105-175	10-73	
April	7.5-54	84-214	18-52	107-162	15-75	95-280	20-74	105-184	19-79	
May	11-94	97-215	23-82	88-147	30-100	120-260	20-89	125-189	25-85	
June	29-119	122-198	33-(132)		40-130	135-270	60-89	145-164	31-103	
July	43-127	130-228	23-(152)		45-(170)	(170)-280	60-99	145-159	48-118	
August	67-139	140-219	48-117	153-157	45-(175)	(175)-280	75-99	165-169	49-103	
September	81-153	155-234	73-132	148-152	65-150	150-265	100-109		52-82	
October	92-170	175-269	78-127		80-150	150-250	70-124	145-169	52-97	
November	90-188	190-264	78-127		75-115	120-250	85-129		67-91	
December	1.5-9.2	84-188	83-147	168-192	65-95	100-260			76-109	

Author	Nelson 1969		Parker 1971		Pearson 1929		Sundararaj 1960		Dunham 1972	
Locality	Mobile Bay, Ala.		Galveston Bay, Tex.		Sabine River to Rio Grande, Tex.		Lake Pontchartrain, La.		Louisiana coast	
Period	May 1963-Apr. 1964		Jan. 1963–Dec. 1965		Mar. 1926–May 1927		July 1953–May 1955		July 1969–June 1972	
Gear[1]	16-ft T		4.0-m T		Tr, T, S, and G		T, Tr, S, and R		16-ft T	
Source	Table 9		Table 2		Table 31		Fig. 17		Fig. 21	
Length (mm)	Total length		Total length		Total length		Total length		Total length	
Age-group[2]	0	I	0	I	0	I	0	I	0	I
January		75-160		60-170			15-25	90-165		100-170
February		90-125	30	70-180			15-40	115-165	10-80	110-170
March		90-180	10-30	60-190			10-75	140-230	20-100	110-170
April	45-70	90-165	10-70	90-160	10-90	120-250	30-100	140-255	40-110	
May	45-(125)	(130)-171	30-100	110-190	40-120	130-250	45-120	(120)-240	50-125	
June	50-140	170-180	30-110	140-190	70-(150)	(150)-230	55-145	150-255	50-155	
July	55-145	200	30-140	170	80-140	150-230	40-160	165-250	20-155	
August	80-135		30-150	170-180	110-(220)	230-270	85-(180)	(180)-215	70-160	
September			30-160		110-(240)	250-260	95-(150)	(150)-210	90-170	110-210
October	95-(190)		50-160		110-(170)	(170)-260	90-150	170-190	120-160	
November	95-165		60-150		130-190	200-250	110-(170)	(170)-205	100-180	
December	90-175	200	70-180		130-190	200-250	135-165		70-180	

[1]Gear: G, gill net; P, pound net; Pl, plankton net; Pu, push net; R, rotenone; S, seine; T, trawl; Tr, trammel net.
[2]Age-group: 0 represents smallest group of young-of-the-year first taken from January on, other fishes (including overwintering young-of-the-year) are included in age-group I. Parentheses indicate that the boundary of age-group 0 and I is indistinguishable.

and the present study), young-of-the-year spot first entered the estuary in April (Table 1). In upper Chesapeake Bay (Young 1953) and Delaware River (Thomas 1971), young-of-the-year spot probably do not appear until May (Table 1). The smallest young-of-the-year spot from trawl catches are about 15 to 20 mm TL in all areas which indicates that the young-of-the-year spot in northern areas enter the estuary later than in southern areas. When spot first enter estuaries, gear selectivity (Table 1) affects the size ranges of spot captured; beach seines usually catch only the small specimens (Young 1953; Figure 9), but pound nets (Pacheco 1957) and large otter trawls (Music 1974) usually catch larger fishes. Offshore movements of spot during the winter season are

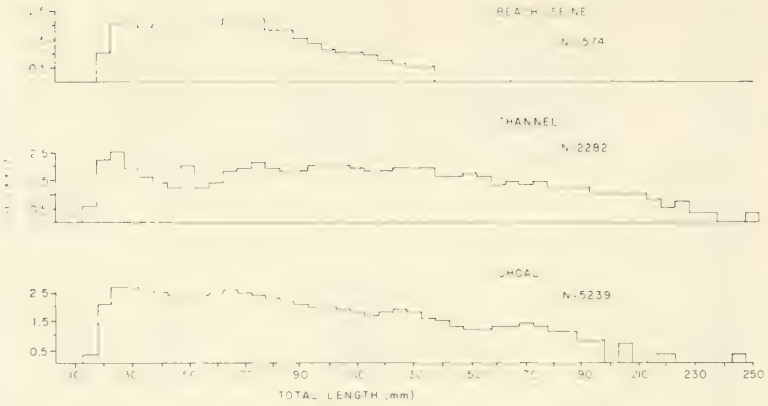


FIGURE 8.—Length-frequency distributions of spot, *Leiostomus xanthurus*, by depth of York River. Pooled total, May to July 1972–74. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

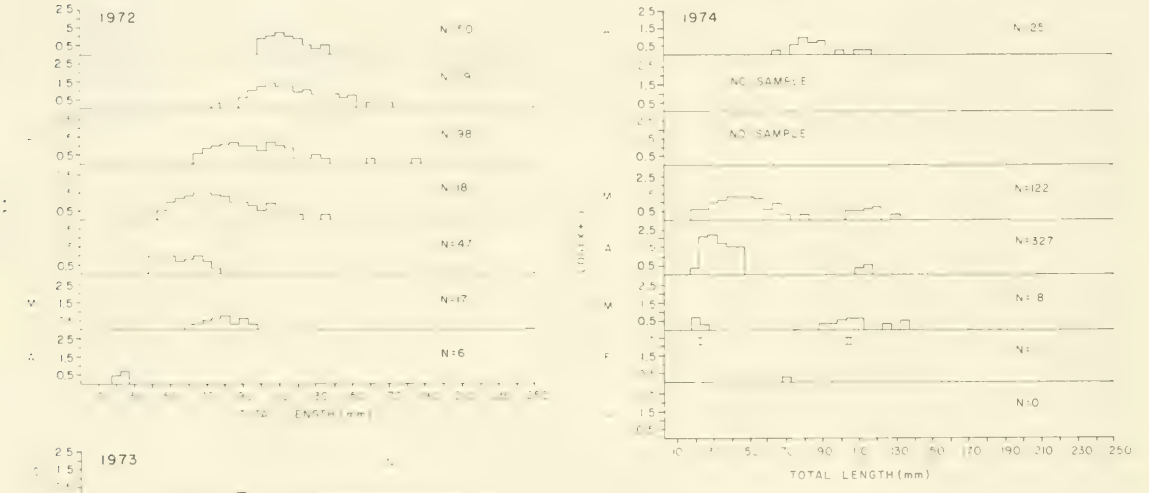


FIGURE 9.—Monthly length-frequency distributions of spot, *Leiostomus xanthurus*, from the beach seine catches of York River, 1972–74. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

evident in all areas studied because spot are completely absent or in low abundance in inshore catches. Yearling or older spot (Table 1, group I) usually leave the estuary after September and do not return until spring of the next year. Some young-of-the-year spot over-winter in the estuary (Figure 6; Table 1). Tagged spot (Pacheco 1962b) have moved from Chesapeake Bay south to an area west of Diamond Shoals, N.C. Similarly, a spot tagged and released from Delaware Bay in October 1930 was recovered south of Ocracoke Inlet, N.C., in December 1930 (Pearson 1932). Thus, spot from these areas may have a common coastal feeding or spawning ground during the winter, although Struhsaker (1969) reported a winter offshore movement of spot into deeper water (lower-shelf habitat off South Carolina). These offshore spot may be a mixture of northern and southern populations or just southern residents. The late fall or early winter spawning time of spot may be the same in both Atlantic and Gulf of

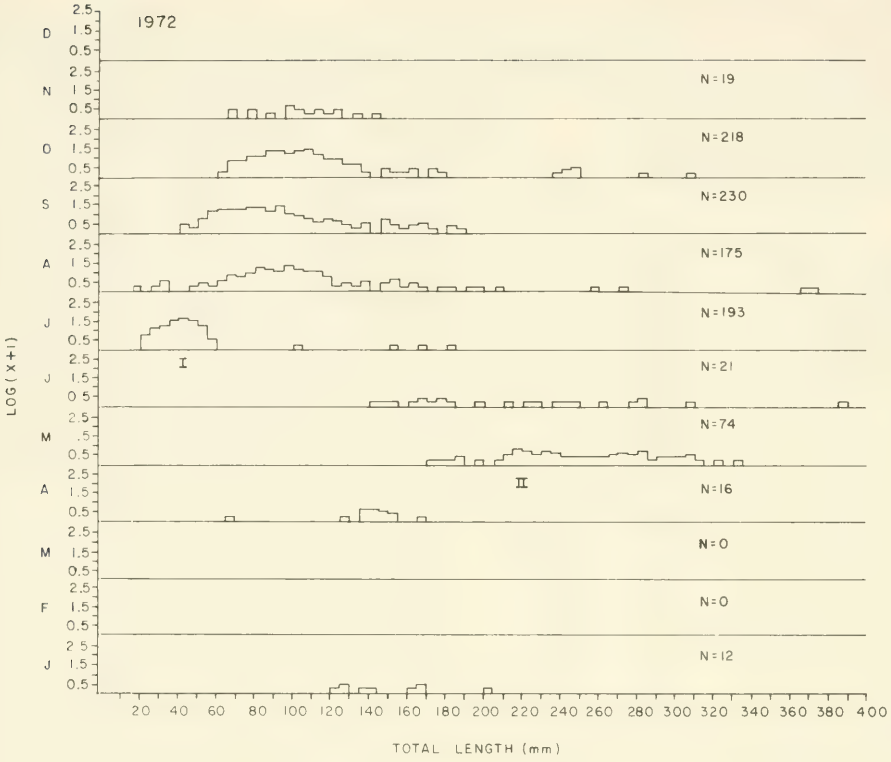
Mexico waters (Welsh and Breder 1923). Later spawning by a northern component of the population is evidenced from the length ranges of postlarvae and juvenile spot (Table 1).

Cynoscion regalis (Bloch and Schneider) — Weakfish

EARLY LIFE HISTORY IN YORK RIVER.—Young-of-the-year weakfish first entered trawl catches in July or August and virtually left the estuary in the winter (Figure 10, mode I). Yearling weakfish returned to the river in April or May and left in September or October (Figure 10, mode II). Larger weakfish (2 yr or older) were caught only sporadically during this study because of gear avoidance. The length mode of small weakfish in August showed a rapid increase (Figure 10). This increase may be due to the recruitment of yearlings or an earlier spawned group of young-of-the-year. Length frequencies for weakfish (<250 mm TL) caught from August to October 1972–74, were pooled to compare distribution by size in the York River and its tributaries (Figure 11). Smaller fishes were more abundant in the Pamunkey and Mattaponi rivers than in the York River proper. Yearling weakfish also showed a movement upriver (Figure 11). This suggests that young weakfish entered the low salinity nursery ground (upper portion of the York River) and then moved downriver as they grew. Pooled length frequency distributions revealed an apparent difference between shoal and channel areas of the York River (Figure 12). Yearling weakfish (or larger ones) were proportionally more abundant in the channel. The 15.25-m beach seine catches contained no weakfish, but occasionally the 30.5-m seine caught some young-of-the-year weakfish in the summer.

OTHER STUDIES.—Major populations of weakfish are confined to the Atlantic coast of the United States from New York to Georgia. Existing data indicate young-of-the-year weakfish enter estuarine or coastal catches from May to July (Table 2). The smallest sizes of the weakfish in the catches differ with area and may be due to gear and/or time of sampling. Small fishes with less size variation (about 5 mm) were taken over a longer period of time in southern areas than northern areas (Table 2). Young-of-the-year weakfish do not occur in catches during winter months in northern coastal areas or estuaries (Perlmutter 1956; Massmann et al. 1958; Thomas 1971; Markle 1976). Year-round catches of weakfishes from North Carolina (Hildebrand and Cable 1934) and Georgia (Mahood 1974) were from sounds and short coastal rivers. Most of the studies suggest the age-group 0 on Table 2 was a combination of young-of-the-year and yearlings. No distinct mode could be identified for young-of-the-year from these studies. This may be due to the multiple spawning (Merriner 1973, 1976) and/or the recruitment of the young-of-the-year from different spawning populations.

The reproductive biology of weakfish is better known than other sciaenid fishes studied here. Welsh and Breder (1923) described the eggs and development of weakfish and noted that Delaware Bay was a spawning ground for weakfish. Merriner (1973) indicated that weakfish have an extended spawning season in North Carolina (March–August) and are characterized by high fecundity and possible multiple spawning by some females. Pearson (1941) took plankton tows in lower Chesapeake Bay from May to August in 1929 and 1930 and reported greater densities of weakfish larvae (1.5–17 mm TL) in subsurface tows (average 67/tow) than in surface tows (average 13/tow). The density of planktonic weakfish decreased at those stations within Chesapeake Bay, compared with sites near the bay mouth. Harmic (1958) reported that newly hatched larval weakfishes averaged 1.8 mm TL. Soon after hatching, the larvae became demersal and were dispersed into the nursery areas of Delaware Bay by means of the "salt wedge." The smallest weakfishes taken in the bottom trawl were 6 to 10 mm TL (Hildebrand and Cable 1934). The young-of-the-year weakfish in York River are probably progeny from adults spawning near the mouth of Chesapeake Bay. Weakfish tagged and released in lower Chesapeake Bay (Nesbit 1954) were later recovered to the north in New York and New Jersey, and southward in North Carolina. Nesbit (1954), Perlmutter et al. (1956), and Harmic (1958) cited the presence of a northern spawning population in New York and northern New Jersey waters and a southern spawning population from New Jersey to North Carolina. Seguin (1960) found that morphometric and meristic variation of weakfish exists along the middle Atlantic coast and suggested that three possible population segments may exist: a New York group, a Delaware and lower Chesapeake group, and a North Carolina group. Joseph (1972) questioned the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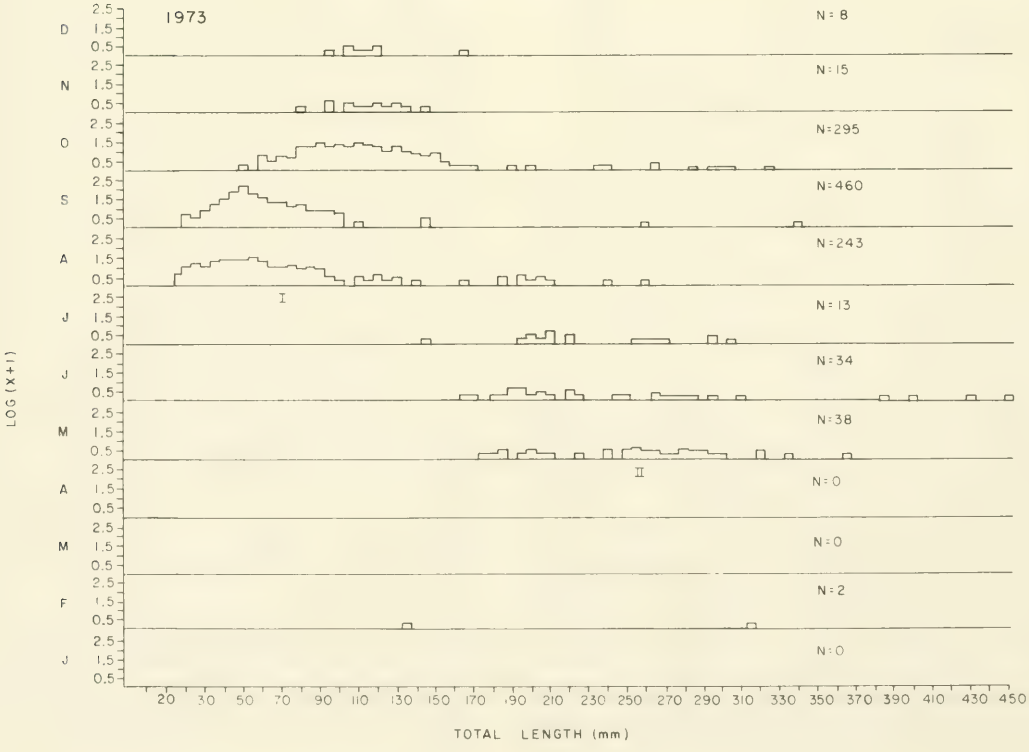
TOTAL LENGTH (mm)


1973
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N=243
N=13
N=34
N=38
N=0
N=0
N=2
N=0
I
II
LOG (X+1)
2.5
1.5
0.5
20 30 50 70 90 110 130 150 170 190 210 230 250 270 290 310 330 350 370 390 410 430 450
TOTAL LENGTH (mm)

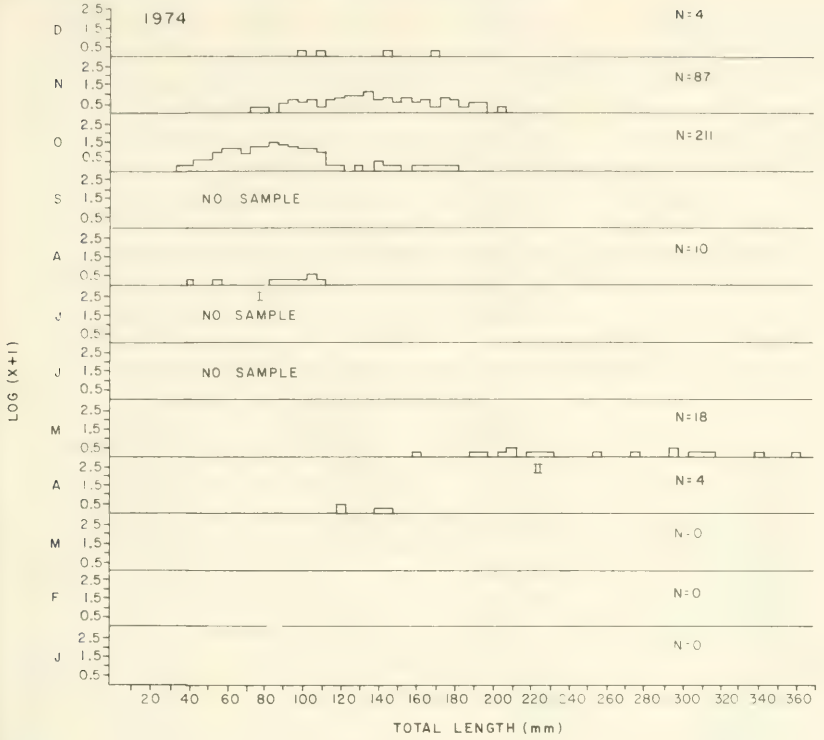


FIGURE 10.—Monthly length-frequency distributions of weakfish, *Cynoscion regalis*, from York River, 1972–74. Mode I, young-of-the-year; mode II, yearlings. Frequencies expressed as log $(x + 1)$ at 5-mm increments. Only the lower portion of river (strata A–D) is represented in 1974.

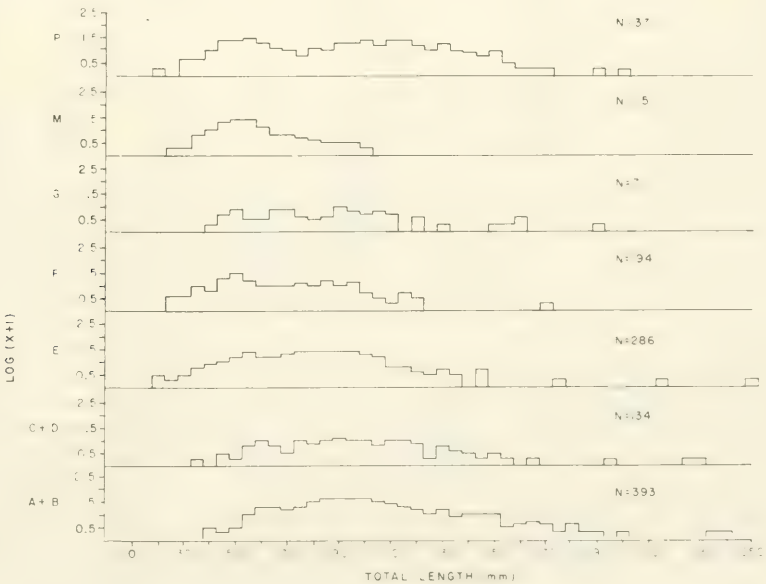


FIGURE 11.—Length-frequency distributions of weakfish, *Cynoscion regalis*, by river distance (strata) upstream of the York River estuary. Pooled total, August to October 1972–74. Strata: A–G in York River, M = Mattaponi River, P = Pamunkey River. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

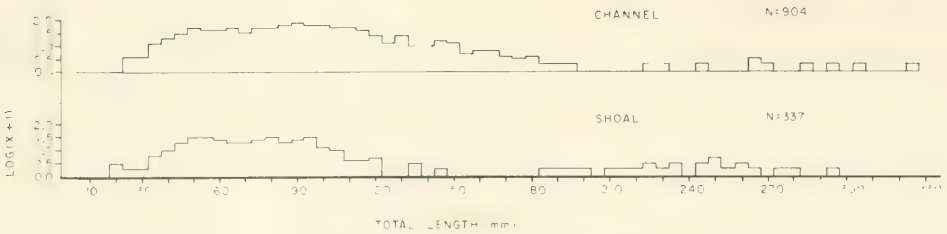


FIGURE 12.—Length-frequency distributions of weakfish, *Cynoscion regalis*, by depth of York River. Pooled total, August to October, 1972–74. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

TABLE 2.—Growth of weakfish, *Cynoscion regalis*, from different estuarine areas along U.S. Atlantic coast.

Author	Thomas 1971		Pearson 1941		Chao 1976	
Locality	Delaware River, Del.		Lower Chesapeake Bay		York River, Va.	
Period	1969		1929-30		Jan. 1972-Dec. 1974	
Gear[1]	T and S		Pl and P		16-ft T	
Source	Table 4		Fig. 23		Fig. 10 (present study)	
Length (mm)	Total length		Total length		Total length	
Age group[2]	0		0	I	0	I
January						120-205
February						130-315
March						
April				130-250		65-175
May						155-330
June	5-70					140-385
July	15-125		20-(150)		20-55	105-305
August	15-(185)		30-(160)		10-(95)	100-370
September	70-(185)			(130)-180	70-(110)	115-300
October	40-(175)				35-(135)	140-325
November					65-(140)	140-205
December					95-(170)	

Author	Hildebrand and Cable 1934		Shealy et al. 1974		Mahood 1974	
Locality	Beaufort, N.C.		South Carolina coast		Georgia Coast	
Period	?		Feb. 1973-Jan. 1974		Oct. 1970-Sept. 1973	
Gear[1]	Pl, P, and T		20-ft T		40-ft T	
Source	Table 4		Table 32		Table 7	
Length (mm)	Total length		Total length		Total length	
Age group[2]	0	I	0	I	0	I
January		75-204		138-327		68-438
February		105-274				68-388
March		90-230		155		83-358
April		80-284		118-188		78-408
May	4-9	125-224				48-358
June	4-44	95-279	23-47	72	13-(128)	(133)-328
July	4-(39)	40-379	23-(52)	(53)-187	18-(173)	(178)-363
August	4-(64)	65-369	23-(72)	(73)-182	23-(203)	(208)-323
September	10-(79)	80-314	23-(67)	(68)-208	18-(213)	(218)-388
October	45-(94)	100-329	28-(72)	(73)-228	28-(223)	(228)-313
November	45-(99)	(100)-329	68-72	78-702	48-(233)	(238)-348
December	85-(94)	(95)-299	88-92	108-197	53-(233)	(238)-348

[1]Gear: P, pound net; Pl, plankton net; S, seine; T, trawl.

[2]Age-group: 0 represents smallest groups of young-of-the-year taken from January on, other fishes (including overwintering young-of-the-year) are included in age-group I. Parentheses indicate that the boundary of age-groups 0 and I is indistinguishable.

division of weakfish into northern and southern stocks and did not consider the decline of weakfish in Chesapeake Bay to be a result of the trawl fisheries in the shallow coastal waters and bays of North Carolina. He indicated Chesapeake Bay as a major spawning area and nursery ground, but also cited failure to obtain one weakfish larva/tow in extensive VIMS ichthyoplankton studies during 1959–63. However, weakfish eggs and larvae were reported from Chesapeake Bay by Hildebrand and Schroeder (1928) and Pearson (1941). Massmann (1963) implied that Chesapeake Bay weakfish are from southern spawning populations or stocks. Therefore, the question remains whether lower Chesapeake Bay and nearshore waters are a major spawning ground for weakfish

(Merriner 1976). Pearson (1932) described the winter trawl fishery off North Carolina and cited higher total catches of weakfish from area B (southwest of Cape Hatteras) than from area A (northeast of Cape Hatteras) in deeper waters. It is possible that most young-of-the-year and larger weakfish that leave the York River move southward to their wintering ground off Cape Hatteras. In spring, weakfish disperse from the wintering ground. Some fish move north and spawning may occur from late spring to summer along the coast from North Carolina to New York.

Bairdiella chrysoura (Lacepède)—Silver Perch

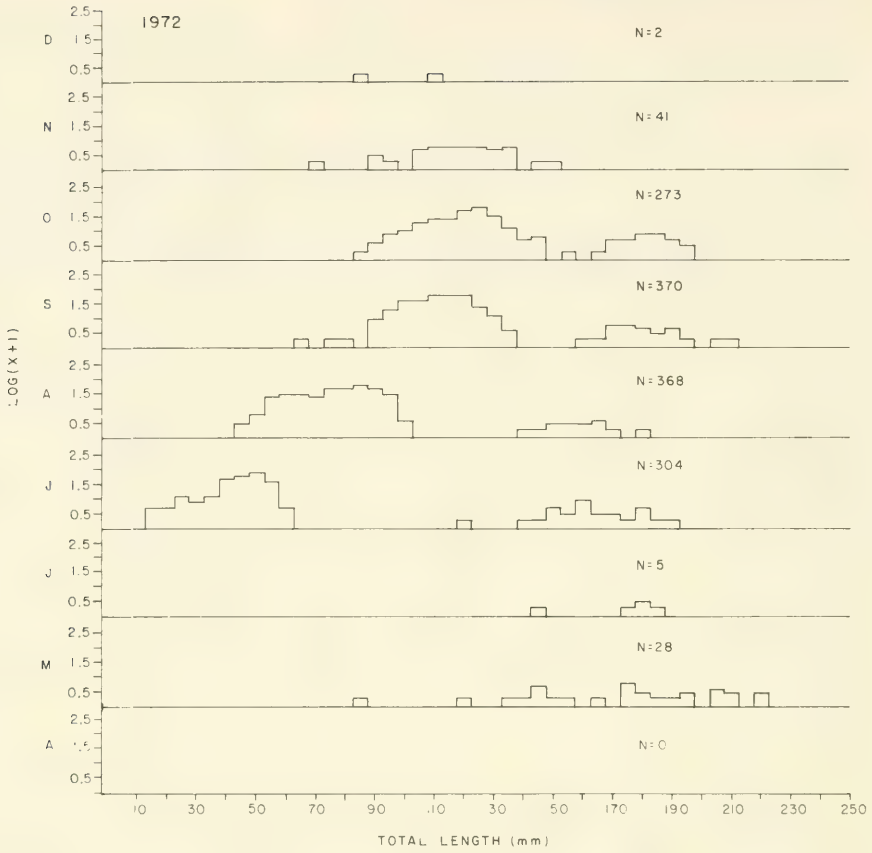
EARLY LIFE HISTORY IN THE YORK RIVER.—Silver perch were present from April to December and were most abundant from August to October (Figure 13). Total catches were reduced in 1973 and 1974. Young-of-the-year silver perch first entered the catches in July and most silver perch left the river in November. Yearlings may enter the river as early as April and most left the river in November. There were no silver perch taken from January to March during the present study (1972-74). Pooled length frequencies from August to October, 1972 to 1974, indicated that silver perch were most concentrated in the lower part of the York River (Figure 14) and larger specimens tended to stay in the channel (Figure 15). The 30.5-m beach seine caught young-of-the-year occasionally but the 15.25-m seine rarely caught any silver perch.

OTHER STUDIES.—Silver perch occur along the U.S. coast from New York to Texas. The seasonal distribution pattern is similar in all Atlantic coastal states (Table 3). Young-of-the-year silver perch were first caught in bottom trawls during June or July. Size of the smallest young-of-the-year silver perch during a given month decreases as latitude of the nursery ground increases on the Atlantic coast and west coast of Florida (Table 3). Silver perch are present almost all year round south of Chesapeake Bay (Table 3), which may be due to the higher salinity or temperature of those study areas. The embryonic development of silver perch from Beaufort, N.C., was described by Kuntz

TABLE 3.—Growth of silver perch, *Bairdiella chrysoura*, from different estuarine areas along U.S. Atlantic and Gulf of Mexico coasts.

Author	Thomas 1971		Chao 1976		Hildebrand and Cable 1930	
Locality	Delaware River, Del.		York River, Va.		Beaufort, N.C.	
Period	1969		Jan. 1972-Dec. 1974		Spring 1926-Summer 1927	
Gear[1]	16 ft T		16 ft T		PI and T	
Source	Table 28		Fig. 13 (present study)		Tables 5 and 6	
Length (mm)	Total length		Total length		Total length	
Age-group[2]	0		0	I	0	I
January						74-204
February						90-209
March						98-204
April						93-195
May				85-200	1-6	85-204
June	5-20			145-185	1-38	110-210
July	5-65		20-60	120-190	9-76	105-224
August	45-100		15-85	100-205	20-92	130-204
September	70-120		65-135	160-210	45-122	135-189
October	65-130		60-135	160-220	73-115	145-224
November			70-155	210	68-143	150-229
December			73-110		78-124	
Author	Shealy et al. 1974		Springer and Woodburn 1960		Reid 1954	
Locality	South Carolina coast		Tampa Bay, Fla.		Cedar Key, Fla	
Period	Feb. 1973-Jan. 1974		Oct. 1957-Dec. 1958		June 1950-May 1951	
Gear[1]	20 ft T		T, S, and Pu		15 ft T, S, and Pu	
Source	Table 42		Fig. 12		Fig. 10	
Length (mm)	Total length		Standard length		Standard length	
Age-group[2]	0	I	0	I	0	I
January	18-(72)	93-182		67		55-60
February		88-137		52-76		
March		98-172		67-73		65-95
April		73-182				
May		113-152	13-25		5-40	84-110
June		123-132	16-52		15-50	
July	33-87	128-192	16-70		20-70	
August	58-107	143-172	16-82		5-80	
September	73-132	138-177	25-85		10-82	
October	78-(187)		28-91		40-95	
November	98-(172)		19-97		50-70	
December	98-(182)		46-106			

[1]Gear: Pl, plankton net; Pu, puchnet; S, seine; T, trawl.
[2]Age-group: 0 represents smallest group of young-of-the-year first taken from January on, other fishes (including overwintering young-of-the-year) are included in age-group I. Parentheses indicate that the boundary of age-groups 0 and I is indistinguishable.



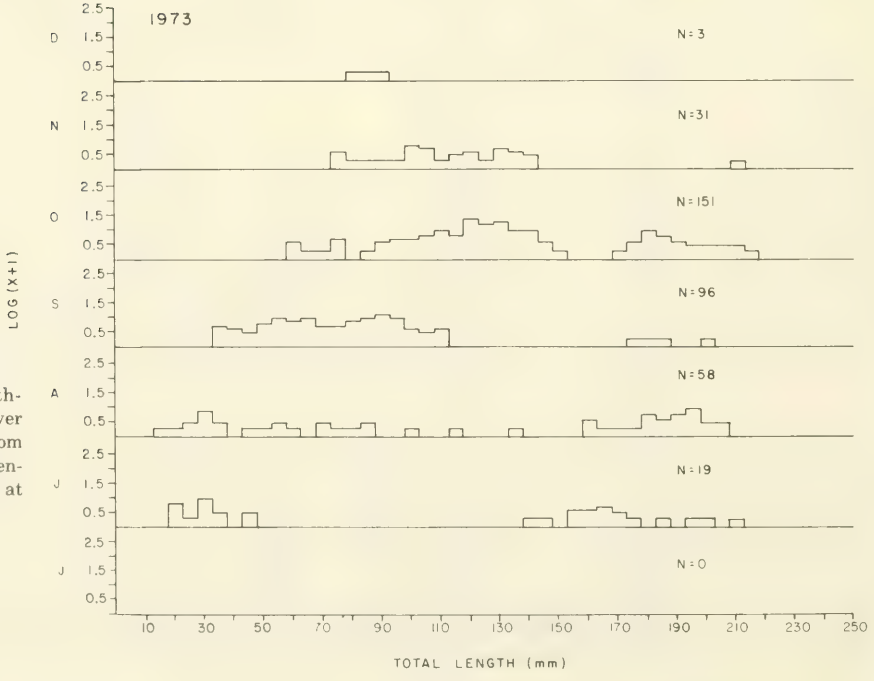


FIGURE 13.—Monthly length-frequency distributions of silver perch, *Bairdiella chrysoura*, from York River, 1972–73. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

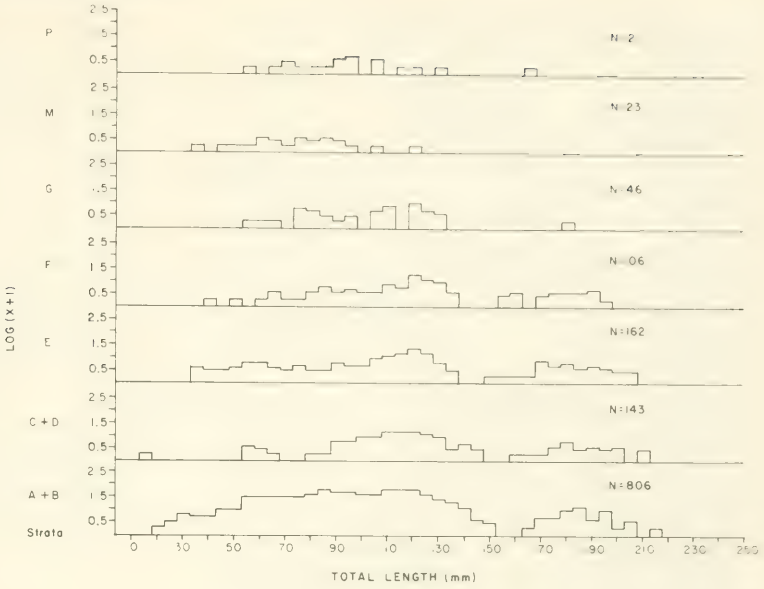


FIGURE 14.—Length-frequency distributions of silver perch, *Bairdiella chrysoura*, by river distance (strata) upstream of the York River estuary. Pooled total, August to October 1972–74. Strata: A–G in York River, M = Mattaponi River, P = Pamunkey River. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

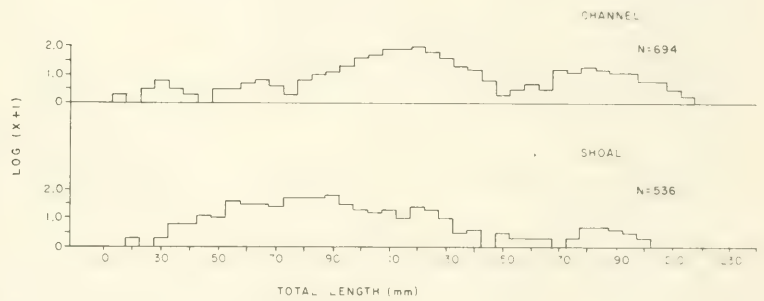


FIGURE 15.—Length-frequency distributions of silver perch, *Bairdiella chrysoura*, by depth of York River. Pooled total, August to October 1972–74. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

(1914). Welsh and Breder (1923) made further observations from material obtained at Atlantic City, N.J. Jannke (1971) described larval silver perch from the Everglades National Park, Fla., and showed that larvae of 2 to 3 mm "notochord" length were present all year round. Hildebrand and Schroeder (1928) reported ripe fish of both sexes in Chesapeake Bay (24 m deep, off Chrisfield, Md.) as early as 16 May. This suggests that silver perch may spawn in the deeper waters of lower Chesapeake Bay and nearshore waters in late spring and early summer. Because of its relatively small size, commercial landings of silver perch are relatively small. Silver perch move oceanward and probably to the south of Chesapeake Bay in winter. Large numbers captured by commercial haul seines between Virginia Beach, Va., and Kitty Hawk, N.C., have been observed in fall (J. A. Musick, pers. obs.).

Micropogonias undulatus (Linnaeus)—Atlantic Croaker

EARLY LIFE HISTORY IN YORK RIVER.—Young-of-the-year croaker first entered the trawl and beach seine catches in August and stayed in the York River throughout the winter (Figure 16, mode I). They left the estuary between August and September of the following year as yearlings (Figure 16, mode III). Large croaker (more than 1.5 yr old) were caught only sporadically in this study due to gear avoidance, but they were present from February to September. There were apparently two to three length groups (modes) of young-of-the-year croaker in September 1972–74. Mode II was different from mode I and mode III of 1972 and 1974 (Figure 16). The former group did not stay in the York River over winter, but entered the estuary as early as May (Figure 16, mode II). Most of this group left in November 1972–74.

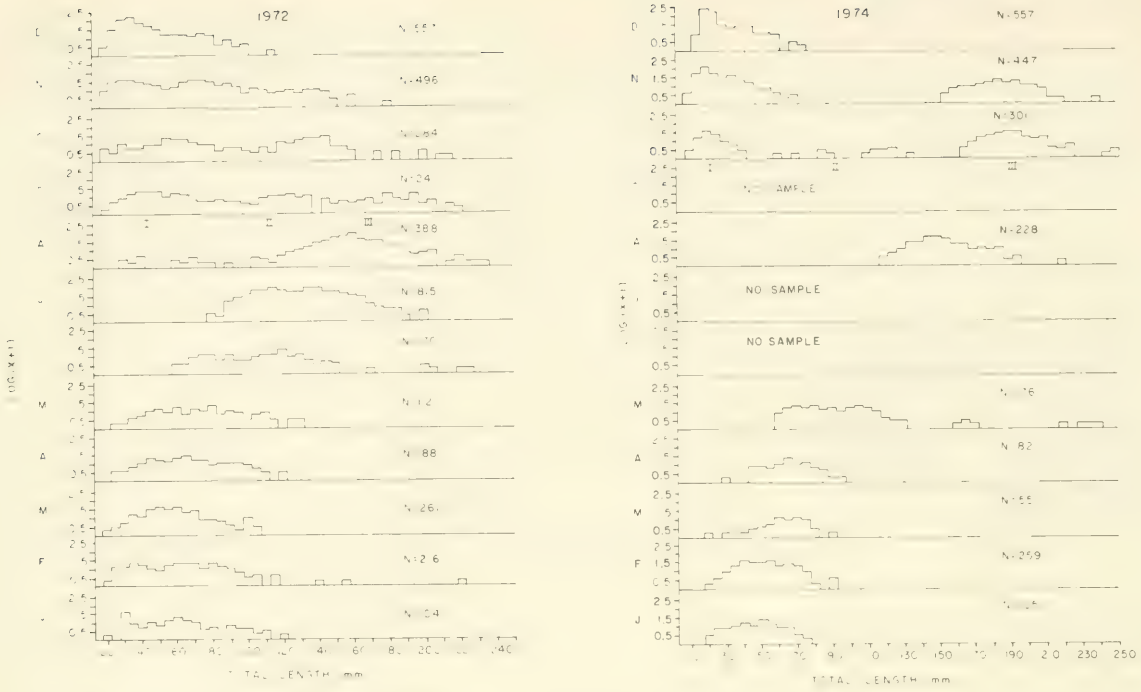


FIGURE 16.—Monthly length-frequency distributions of croaker, *Micropogonias undulatus*, from York River, 1972–74. Modes I and II, young-of-the-year; mode III, yearling. Frequencies expressed as log $(x + 1)$ at 5-mm increments. Only the lower portion of river (strata A–D) is represented in 1974.

Size may be a determining factor for migration of young croakers from the York River. From 1972 to 1974, length frequencies (Figure 16) indicated that very few young-of-the-year croakers >130 mm TL stayed in the York River during the winter months. Young-of-the-year croakers were present in the York River in large numbers all year round except during the summer months (June–August). Young croakers showed slower growth rates over winter (Figure 16). Those entering the estuary between September and November were the main strength of the year class (modes I and III of Figure 16). Whether they represent progeny from a different spawning population compared with the earlier group (mode II of Figure 16) is unknown at present.

Length frequencies of croakers taken between September and November 1972–74 were pooled to compare distribution by size in the York River (Figure 17). The size composition indicated that smaller fish were caught in the upper part of the York River and saline portions of the Mattaponi and Pamunkey rivers. Larger fish were proportionally more abundant in the lower part of the river. Larger fish also constituted a larger portion of the croaker catch in the channel than in the shoal area (Figure 18). The 30.5-m beach seine

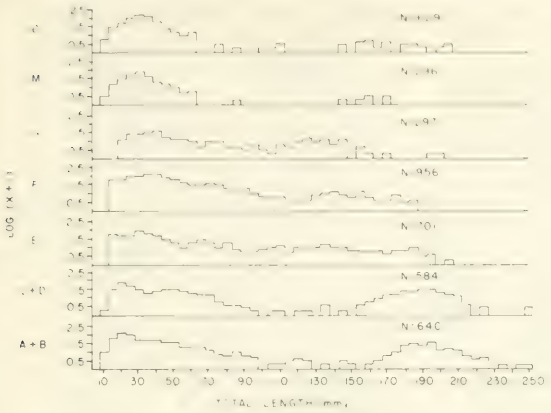


FIGURE 17.—Length-frequency distributions of croaker, *Micropogonias undulatus*, by river distance (strata) upstream of the York River estuary. Pooled total, September to November 1972–74. Strata: A–G in York River, M = Mattaponi River, P = Pamunkey River. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

(Figure 19) caught yearlings exclusively. The 15.25-m seine caught almost no croakers.

In summary, young-of-the-year croaker entered the estuary in May and from August on. The earlier group entered in May and left the estuary in November, as did older year classes. The later group (August–November) stayed in the estuary until the summer months of the following year. Young croaker moved to the upper part of the York River and the saline portions of major tributaries after first entry, then moved down the York River into more saline waters as they grew. Smaller fishes (<130 mm TL) stayed in the river throughout the winter.

OTHER STUDIES.—Croakers occur from the Gulf of Maine to Argentina, along the coasts of the Atlantic and Gulf of Mexico. Length-frequency distributions exist for different areas of the United States [see Wallace (1940) and Haven (1957) for the lower Chesapeake Bay and York River (Table 4)]. Studies usually show that small croakers (10–20 mm TL) are present in the estuary during all except the summer months (June–August). Croakers seemingly have a long spawning season since small individuals (<20 mm TL) are present from September to May in different estuarine areas (Table 4). Some croakers may be very small (<15 mm TL) in spring because of slow growth of fish spawned late in winter, or because they were spawned in spring. Such a group was also found in the present study (Figure 16, mode II) but not in previous Chesapeake Bay studies. Croakers from Maryland and Virginia tagged by Haven (1959) showed springtime movement of croakers up the estuaries and up Chesapeake Bay, and oceanward and southerly in fall (some recoveries were from off the North Carolina coast). Pearson (1932) reported a high percentage of croakers in the catches of the commercial trawl fishery during November (88%) and December (76%) from the fishing grounds off the North Carolina coast. Hildebrand and Cable (1930) implied that croaker spawning probably began in August in Chesapeake Bay and northward, in September at Beaufort (North

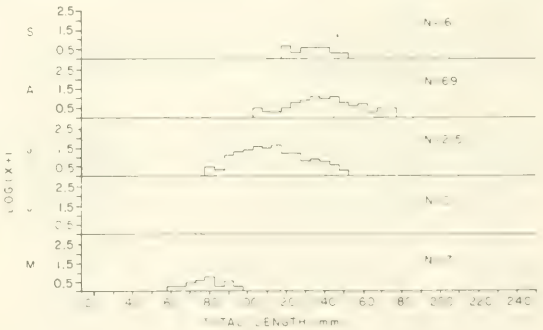


FIGURE 19.—Length-frequency distributions of croaker, *Micropogonias undulatus*, from beach seine catches of York River, May to September 1972. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

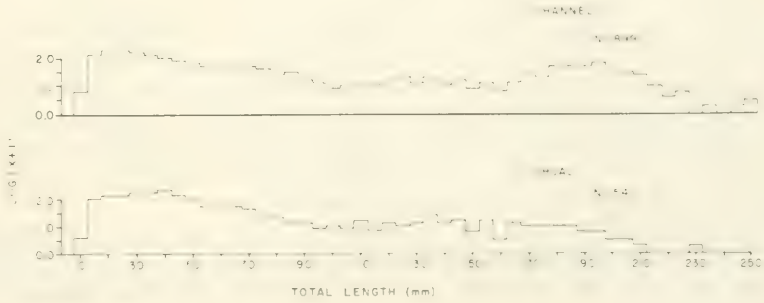


FIGURE 18.—Length-frequency distributions of croaker, *Micropogonias undulatus*, by depth of York River. Pooled total, September to November 1972–74. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

TABLE 4.—Growth of croaker, *Micropogonias undulatus*, from different estuarine areas along U.S. Atlantic and Gulf of Mexico coasts.

Author	Thomas 1971		Haven 1957		Chao 1976		Hildebrand and Cable 1930		Shealy et al. 1974	
Locality	Delaware River, Del.		York River, Va.		York River, Va.		Beaufort, N.C.		South Carolina coast	
Period	June 1968-Dec. 1970		Oct. 1952-July 1953		Jan. 1972-Dec. 1974		Spring 1926-Summer 1927		Feb. 1973-Jan. 1974	
Gear[1]	16-ft T		30-ft T		16-ft T and S		T and PI		20-ft T	
Source	Table 70		Fig. 7		Fig. 16 (present study)		Tables 9 & 10		Table 22	
Length (mm)	Total length		Total length		Total length		Total length		Total length	
Age-group[2]	0	I	0	I	0	I	0	I	0	I
January			15-(85)	(95)-105		20-120	3-24	25-269	18-97	108-297
February			10-60	(45)-100		20-155	3-29	40-294	28-82	113-187
March			10-(70)	(70)-120		20-175	2-24	40-294	13-102	123-173
April			10-(65)	70-100		25-120	25-19	100-259	18-(132)	138-192
May			25-(90)	70-140	20-30	(20)-240	8-25	195-239	28-112	
June			40-(120)	(120)-155	20-70	(60)-245		31-284	33-142	
July			75-145	(135)-175	30-(110)	(80)-250		43-234	28-(182)	
August			N.S.	N.S.	30-(90)	(70)-240		66-289	53-177	
September			N.S.	N.S.	10-(100)	(70)-195	2-9	80-279	78-182	
October	20	135-140	10-(40)	(40)-85	10-(110)	(100)-250	2-50	98-294	68-182	
November	25		15-(60)	(60)-115	15-100	(60)-250	1.5-66	85-284	43-153	
December	20-50		10-(60)	(60)-120	20-110	165-175	2.5-69	85-259	48-163	183-197

Author	Hoese 1973		Hansen 1969		Suttkus 1955		Parker 1971	
Locality	Georgia coast		Pensacola, Fla.		Lake Pontchartrain and Louisiana coast		Galveston Bay, Tex.	
Period	Aug. 1956-Aug. 1966		Aug. 1963-Dec. 1965		July 1953-Oct. 1954		Jan. 1963-Dec. 1965	
Gear[1]	30- and 40-ft T		5-m T		T and S		4.9-m T	
Source	Fig. 12		Fig. 2		Table 1		Fig. 21	
Length (mm)	Total length		Total length		Total length		Total length	
Age-group[2]	0	I	0	I	0	I	0	I
January	10-80	120-130	15-20	45-95	10-79	120-189	10-(80)	90-200
February	20-80		20-25	40-95	10-89	130-179	10-(90)	(90)-250
March	20-80	110-120	15-35	75-85	20-119	120-259	10-(90)	(100)-250
April	40-100		N.S.	N.S.	20-129	130-339	10-(120)	(130)-250
May	20-110		20-(75)	(60)-135	30-139	140-319	10-(130)	(130)-240
June	50-140	200-210	30-(95)	(90)-150	30-139	140-329	40-(140)	(156)-250
July	60-140		35-(90)	(90)-145	50-159	160-380	30-(150)	(160)-230
August	90-160	190-200	35-(110)	(100)-150	80-169	170-319	60-160	170-250
September	60-150		40-(90)	(90)-150	80-169	170-319	60-(170)	(170)-190
October	100-180		45-(110)	(110)-150	90-189	(170)-349	10-40	60-220
November			50-105		20-59	130-309	10-(60)	60-210
December			10-95		10-79	120-299	10-(70)	70-230

[1]Gear: Pl, plankton net; S, seine; T, trawl.
[2]Age-group: 0 represents smallest group of young-of-the-year first taken from January on, other fishes (including overwintering young-of-the-year) are included in age-group I. Parentheses indicate that the boundary of age-groups 0 and I is indistinguishable. N.S.; no sample.

Carolina), and in October in Texas. Arnoldi et al. (1973) "tagged" young-of-the-year croakers (9-48 mm TL). Their successful recaptures indicated that individual croaker remained in the particular marsh for only 1 to 4 mo, which was much shorter than the total length of time croaker were observed in the marsh (October–June). Thus, they also suggested that several croaker "populations" may utilize coastal marsh as nursery ground during the course of the year. White and Chittenden (1977) indicated that some croakers in the Gulf of Mexico may lack the first (overwinter) ring on the scales. This suggests that some croakers may spawn in the spring in the Gulf of Mexico.

Massmann and Pacheco (1960) reported the disappearance of young croakers from the York River, but their conclusion may have been in error because of selectivity of their fishing gear. Haven's (1957) length frequencies for croakers during 1952 and 1953 differ from those presented by Massmann and Pacheco (1960) for the same years. No fish <100 mm TL were reported by Massmann and Pacheco (1960), but their gear was a net with ¾-in (about 1.9-cm) mesh, whereas Haven (1957) used ¼-in (about 0.6-cm) mesh. Joseph (1972) attributed the decline of croaker in the commercial catches of the middle Atlantic coast to climatic trends. Present data support his hypothesis. The apparent increase in juvenile croakers in 1973 and 1974 was probably due to warmer winter months. Mean bottom temperatures of the York River channel were about 3.6°C and 3.2°C in January and February, respectively, from 1967 to 1971 (Markle 1976). It was 6.7°C for January and 6.3°C for February in 1973 and 1974 (Figure 2). The year class strength of croaker in the York River was dependent on the success of the late young-of-the-year group (Figure 16, mode I), which stayed in the estuary through the winter. Historical York River trawl data show mass mortalities of young-of-the-year croaker during some cold winters (VIMS, Ichthyology Department, unpubl. data).

Feeding Mechanisms

The Sciaenidae have the widest spectrum of

feeding niches of any fish family in the Chesapeake Bay. The four most abundant species, *Cynoscion regalis, Bairdiella chrysoura, Micropogonias undulatus,* and *Leiostomus xanthurus,* are most abundant in the estuary from late spring to fall, especially young-of-the-year and yearlings (see previous sections). Under these conditions, food resources may be limiting and division of feeding niches may have evolved in order to reduce competitive exclusion among the dominant species. Fishes that are closely related and show feeding niche segregation also often show morphological differentiation in the feeding apparatus (Keast and Webb 1966; Davis 1967; Keast 1970; Davis and Birdsong 1973; Emery 1973). This section of the paper examines the morphology of the feeding apparatus in *Larimus fasciatus, C. regalis, B. chrysoura, M. undulatus, Menticirrhus saxatilis,* and *Leiostomus xanthurus* to test the hypothesis that adaptations to feeding niche division have evolved among those six species.

Characters important in feeding were examined including mouth position and size, dentition, number of gill rakers, and intestine length. These directly affect the size and kind of food ingested and digested. Other accessory characters examined were the pore and barbel system on the snout and/or lower jaw, the nares, and body shape.

Mouth Position

Mouth position and size of the opening limit the size of prey and habitats in which a predator can effectively capture prey. These characters were

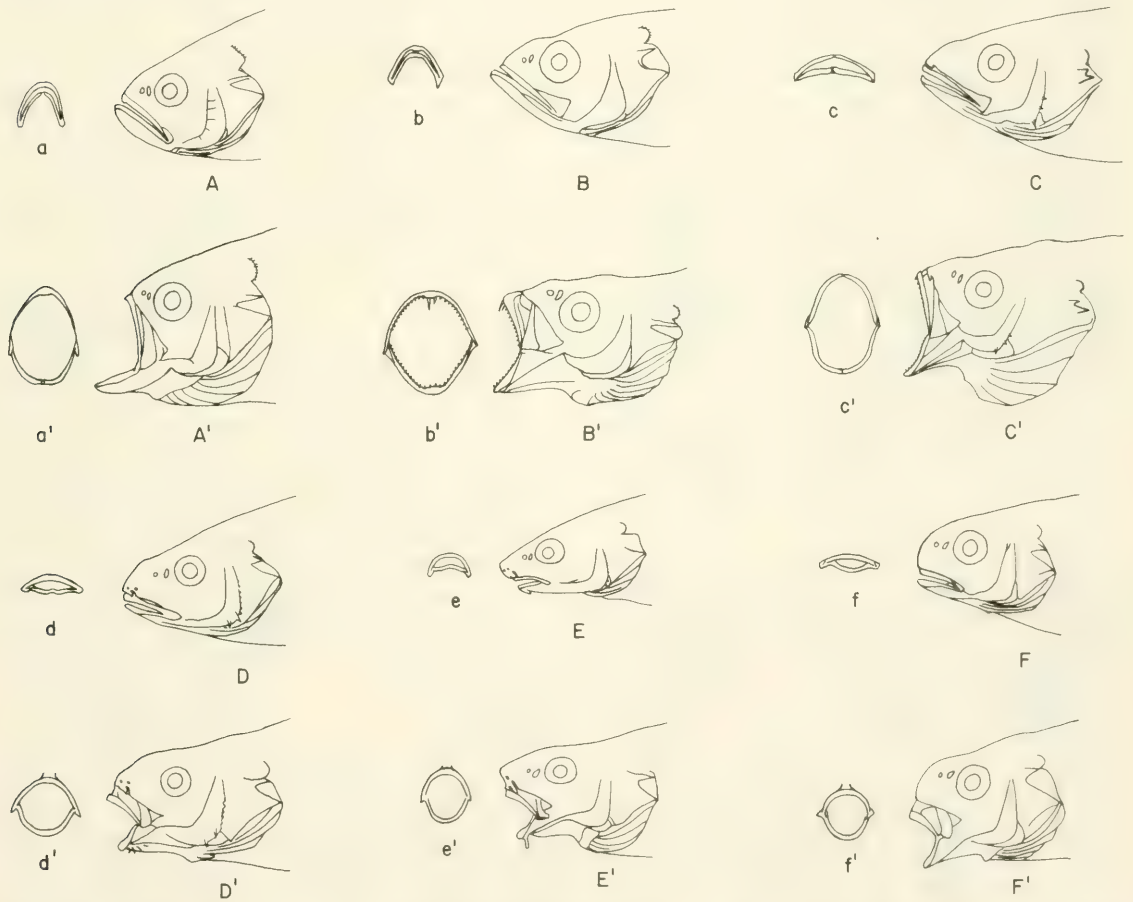


FIGURE 20.—Mouth position and opening in juveniles of six species of sciaenids: A, A′, a, a′, *Larimus fasciatus;* B, B′, b, b′, *Cynoscion regalis;* C, C′, c, c′, *Bairdiella chrysoura;* D, D′, d, d′, *Micropogonias undulatus;* E, E′, e, e′, *Menticirrhus saxatilis;* F, F′, f, f′, *Leiostomus xanthurus.* A–F, mouth closed. A′–F′ mouth wide open. Front view of mouth openings (lower case letters) in corresponding positions.

studied from freshly caught and preserved specimens. *Larimus fasciatus* has the most oblique mouth (Figure 20A) with the lower jaw projecting strongly in front of the nonprotrusible upper jaw. The maxilla (Figure 21A) is under the lateral margin of the rostral fold and its anterior end is firmly attached to the premaxilla and skull (dermethmoid). As the mouth opens, the distal ends of the premaxilla and maxillae push forward as the lower jaw is lowered (Figure 20A′). The mouth opens widely. *Cynoscion regalis* has a large oblique mouth with the tip of the lower jaw projecting in front of the nonprotusible upper jaw (Figure 20B). The anterior end of the maxilla is firmly attached to the premaxilla and articulates with the dermethmoid (Figure 21B). As the mouth is opened, the posterior end of the premaxilla and the lower jaw move forward (Figure 20B′). The mouth opens widely. *Bairdiella chrysoura* has a similar mechanism of jaw movement (Figure 20C′), but the mouth is only slightly oblique with the lower jaw about equal in length to the upper jaw (Figures 20C, 21C). *Micropogonias undulatus* has an inferior mouth with the tip of the lower jaw enclosed by the protrusible upper jaw (Figure 20D). The anterior end of the maxilla is loosely attached to the premaxilla (Figure 21D). As the mouth is opened, the entire premaxilla and the lower jaw move anteroventrally (Figure 20D′). The mouth opens widely. *Menticirrhus saxatilis* and *Leiostomus xanthurus* have a similar mechanism of jaw movement but their upper jaws seem more protrusible (Figures 20E′, F′; 21E, F). Their gape is small. In *M. saxatilis*, the mouth is inferior and the lower jaw is enclosed by the upper jaw (Figure 20E). *Leiostomus xanthurus* also has a small inferior mouth (Figure 20F) with a small gape.

The mouth position indicates that *Larimus fasciatus, C. regalis,* and *B. chrysoura* are pelagic feeders (Figure 20A–C) and that *Micropogonias*

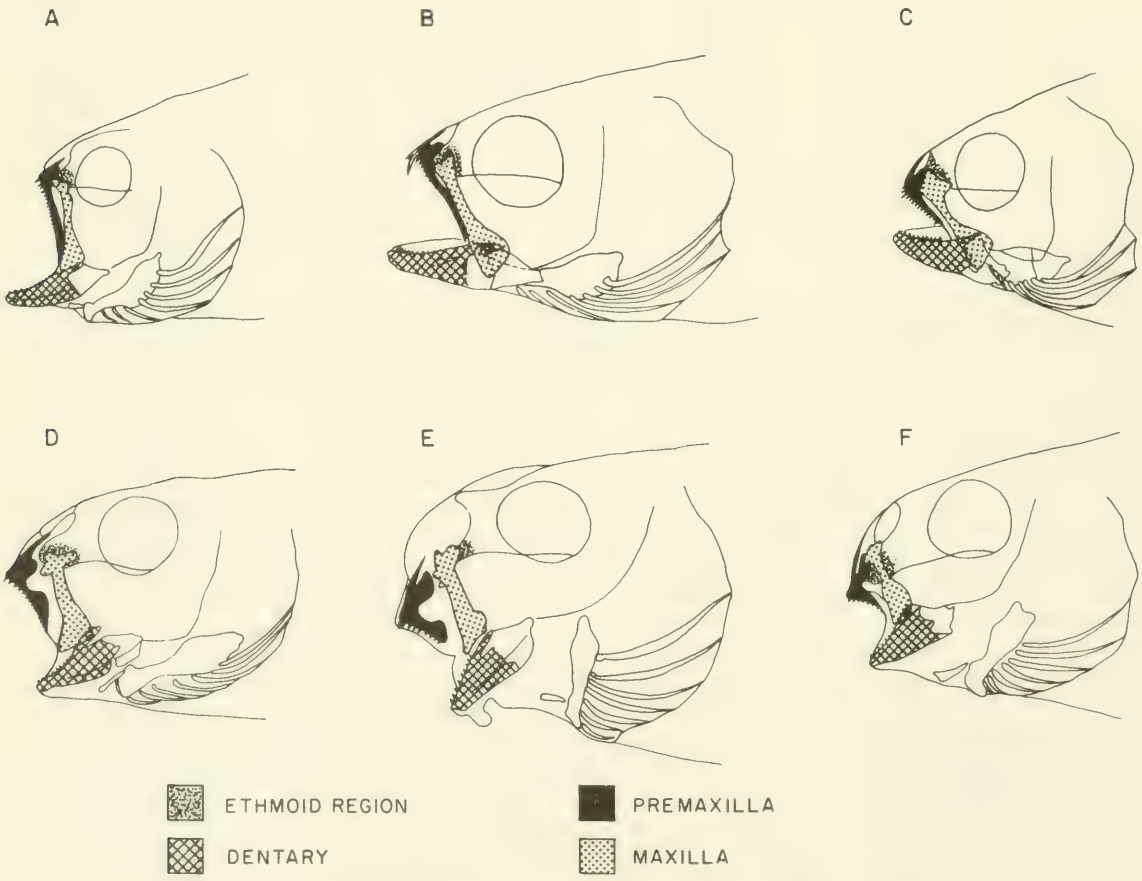


FIGURE 21.—Jaw bones involved in mouth opening in juveniles of six species of sciaenids: A. *Larimus fasciatus*; B. *Cynoscion regalis*; C. *Bairdiella chrysoura*; D. *Micropogonias undulatus*; E. *Menticirrhus saxatilis*; F. *Leiostomus xanthurus*.

undulatus, *Menticirrhus saxatilis*, and *Leiostomus xanthurus* feed on the bottom (Figure 20D–F). The relative length of the premaxilla and dentary bones decreases and the height of the anterior dorsal process of the premaxilla increases from fishes adapted to feed in "midwater" to those adapted to feed on the bottom (Figure 21). This trend is also evident in the relative mouth size and angle (Figure 21A–F). An index number (Table 5), the length of the upper jaw multiplied by the length of the lower jaw then divided by head length, decreases through the series of species towards a bottom feeding habit.

Bottom feeders, *M. undulatus*, *L. xanthurus*, and *Menticirrhus saxatilis*, have protrusible premaxillae (Figures 20D′–F′, 21D–F). This can be advantageous in getting the mouth opening close to food that is to be sucked in from the bottom (Alexander 1967). Midwater feeders, *Larimus fasciatus*, *C. regalis*, and *B. chrysoura*, lack the protrusibility of the premaxillae (Figures 20A′–C′; 21A–C); *C. regalis* and *B. chrysoura* may compensate for this with faster swimming speed. Gero (1952) and Nyberg (1971) have discussed this aspect in detail. *Larimus fasciatus* differs from other sciaenids studied here. It may swim around with its mouth open using its gill rakers as a filter similar to that of *Engraulis* (Günther 1962).

Dentition

Teeth on the premaxilla and dentary are important in capturing prey whereas the pharyngeal teeth are used for grinding and/or transporting food to the esophagus. Members of the genus *Cynoscion* usually have a pair of enlarged canine teeth at the tip of the upper jaw (Figures 21B, 22B). Other teeth are conical and present on narrow bands of the premaxilla and dentary. The tips of the upper and lower jaws are broad and have several rows of teeth which decrease in number to a single prominent row on the narrower posterior portion of the jaws. Small teeth also develop inside the larger row of upper jaw teeth and outside the lower jaw teeth. *Bairdiella chrysoura* has a narrow band of teeth similar to *C. regalis* but lacks large canine teeth at the tip of the upper jaw (Figure 22C). *Micropogonias undulatus*, *Leiostomus xanthurus*, and *Menticirrhus saxatilis* have villiform teeth set in broad bands on the premaxillae and dentaries, and also lack canine teeth (Figure 22D–F). The teeth on the outer row of the premaxillae and inner row of the dentaries are slightly enlarged. *Larimus fasciatus* is unique in having only one or two rows of small teeth on both jaws (Figure 22A).

Pharyngeal teeth are generally conical in sciaenids (Figure 23). The lower pharyngeal teeth form a pair of separate narrow tooth patches and are situated on the most medial pairs of ceratobranchial bones. The upper pharyngeal teeth occur mainly as two pairs of patches on the two most medial pairs of epibranchial bones. The pharyngeal plates are relatively small and narrow in *L. fasciatus* and *C. regalis* compared with the other sciaenids examined (Figure 23A, B). The pharyngeal teeth of *L. fasciatus* and *C. regalis* are sharp, conical, and directed backward, but in *B. chrysoura* the pharyngeal teeth are blunt and the median ones are enlarged (Figure 23C). *Micropogonias undulatus* has much stronger and more enlarged pharyngeal teeth along the median rows (Figure 23D). *Menticirrhus saxatilis* has fine and sharp pharyngeal teeth (Figure 23E). *Leiostomus xanthurus* develops molariform teeth medially on the pharyngeal plates (Figure 23F). These sequential morphological differences in pharyngeal teeth reflect the feeding niche differentiation from midwater to benthic.

Gill Rakers

Gill rakers on the branchial arches of fishes are important in protecting the delicate gill filaments

TABLE 5.—Relative size of mouth and eye diameter in juveniles of six species of sciaenids from the York River.

Species	SL (mm)	Head length (mm)	Index of mouth size[1]				Eye diameter in % of SL			
			Range	$\bar{x}$	SD	N	Range	$\bar{x}$	SD	N
Larimus fasciatus	55.3-107	18.7-36.3	3.17-5.90	4.634	0.957	20	7.38- 9.84	8.602	0.672	21
Cynoscion regalis	35.2- 75.3	12.7-29.6	1.93-3.54	2.827	0.518	22	8.20-11.45	9.55	0.782	26
Bairdiella chrysoura	38.4- 77.5	14.3-27.4	1.76-3.08	2.494	0.431	17	8.27-10.82	9.407	0.677	20
Micropogonias undulatus	35.5-116	12.1-39.3	1.20-2.41	1.686	0.325	30	6.45- 9.46	7.850	0.837	30
Menticirrhus saxatilis	29.2- 99.6	9.3-29.0	0.50-1.37	0.957	0.264	30	6.03- 8.56	7.043	0.644	30
Leiostomus xanthurus	47.4-146	18.0-41.3	0.77-2.64	1.472	0.477	30	7.05-11.11	9 139	0.889	46

[1]Index of mouth size = (upper jaw length × lower jaw length)/head length.

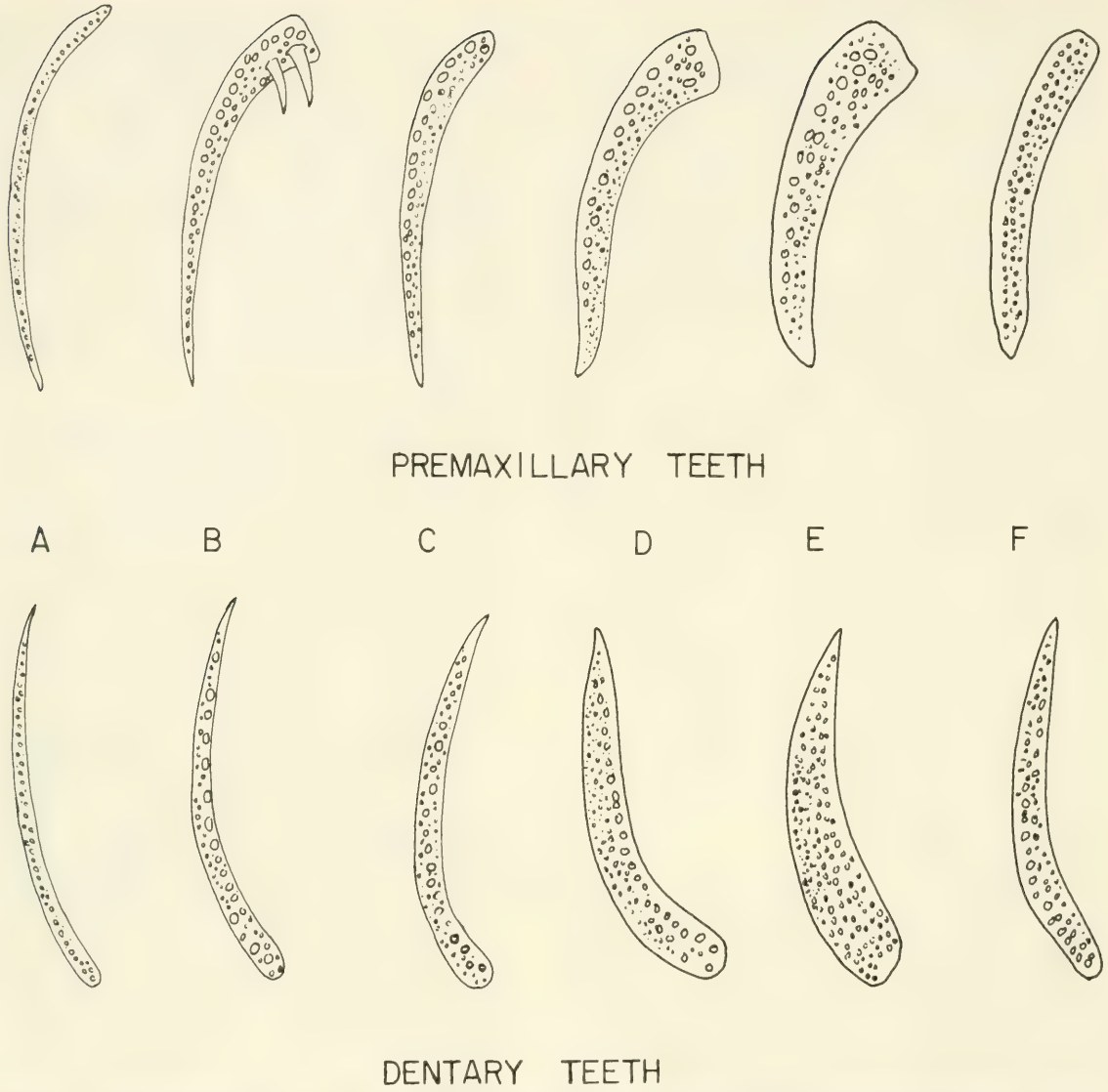


FIGURE 22.—Dentition of right premaxilla and dentary in juveniles of six species of sciaenids: A. *Larimus fasciatus*; B. *Cynoscion regalis*; C. *Bairdiella chrysoura* D. *Micropogonias undulatus*; E. *Menticirrhus saxatilis*; F. *Leiostomus xanthurus*. Posterior end toward the middle of the figure.

from abrasion by ingested materials and may also be adapted to particular food and feeding habits. In sciaenids, the gill rakers reflect feeding niche by their numbers, size, and shape. They are found on the dorsolateral surface of the branchial arch (Figure 24) and along its inner surface. The lateral gill rakers are well developed only on the first gill arch and the inner (or medial) gill rakers occur only as tubercles on all five gill arches. Only the rakers on the first gill arch are discussed here.

Menticirrhus saxatilis and *C. regalis* have the fewest gill rakers (Table 6). *Bairdiella chrysoura* and *Micropogonias undulatus* have an intermediate number and *L. xanthurus* and *Larimus fasciatus* have the most gill rakers. Numbers of inner gill rakers (Table 6) follow a similar sequence. The relative size of the gill rakers and their morphology differ among species (Figure 24).

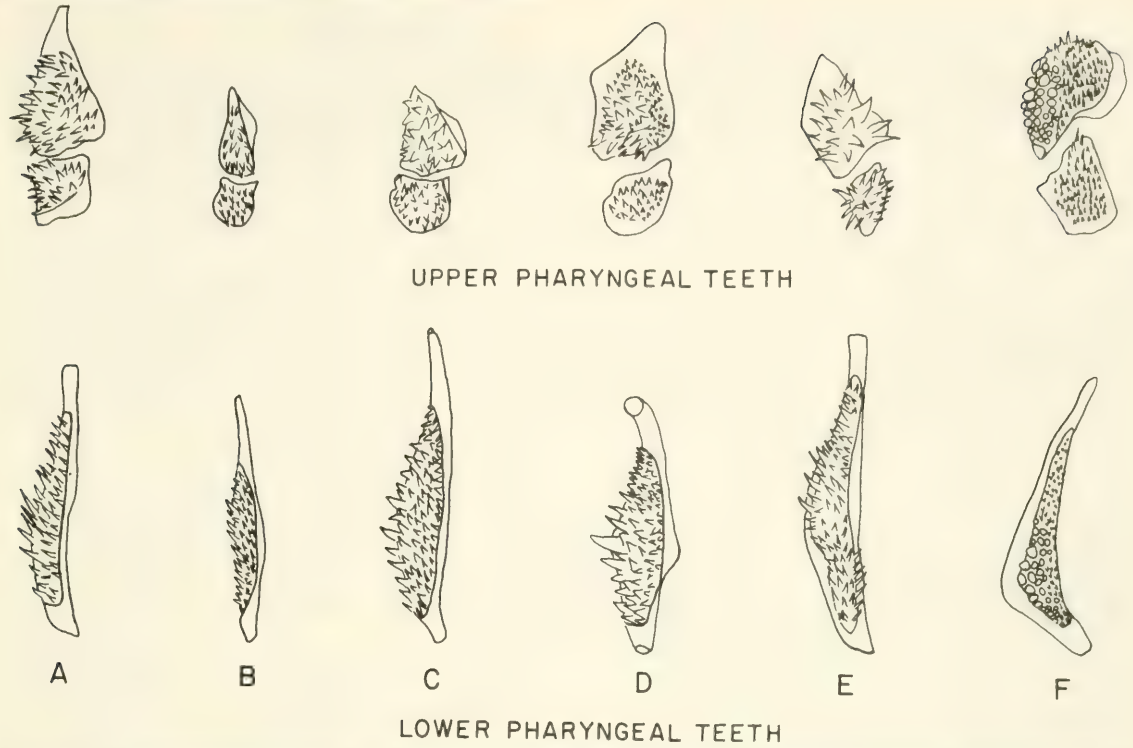


FIGURE 23.—Portions of left pharyngeal teeth in juveniles of six species of sciaenids: A. *Larimus fasciatus*; B. *Cynoscion regalis*; C. *Bairdiella chrysoura*; D. *Micropogonias undulatus*; E. *Menticirrhus saxatilis*; F. *Leiostomus xanthurus*. Posterior end toward the middle of the figure.

TABLE 6.—Total number of lateral and inner gill rakers in juveniles of six species of sciaenids from the York River.

Species (size in mm SL)	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25		N	$\bar{x}$
Menticirrhus saxatilis						6	11	9	3	1												30	12.04
(29.2-99.6)	[5	20	4	—	1]¹																	[30]	[6.73]
Cynoscion regalis										1	8	13	13	2								37	17.19
(35.2-75.3)			[	—	4	10	8	2	2]													[27]	[11.40]
Micropogonias undulatus														1	—	3	16	15	7			42	22.55
(35.5-116)									[2	8	16	4]								1		[30]	[15.73]
Bairdiella chrysoura																2	3	13	14			33	24.27
(38.4-75.3)								[1	2	5	6	6]										[20]	[15.70]

Species (size in mm SL)	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	N	$\bar{x}$
Leiostomus xanthurus												4	7	6	12	9	13	3	1				55	32.29
(47.4-148)						[1	1	4	9	7	14	6	2]										[44]	[27.18]
Larimus fasciatus																		5	9	5	2	1	22	38.00
(55.3-107)	[1	1	5	7	4	2	1]																[21]	[21.04]

¹[] medial gill rakers.

Larimus fasciatus has the longest and the most closely spaced gill rakers (Figure 24A). Each raker has many minute spicules scattered on it (Figure 24a). *Cynoscion regalis* and *B. chrysoura* have moderately long gill rakers compared with the length of the gill filaments (Figure 24B, C). Numerous minute spicules are also present on each raker, especially the basal portion (Figure 24b, c). *Micropogonias undulatus* has relatively shorter gill rakers (Figure 24D) with seemingly strong serrations limited to the basal half of the raker (Figure 24d). The relative lengths of the lateral gill rakers in *Menticirrhus saxatilis* and *Leiostomus xanthurus* are the shortest (Figure 24E, F) and lack strong spicules (Figure 24e, f). *Leiostomus xanthurus* has only slightly denticulate gill rakers and *M. saxatilis* has smooth gill rakers.

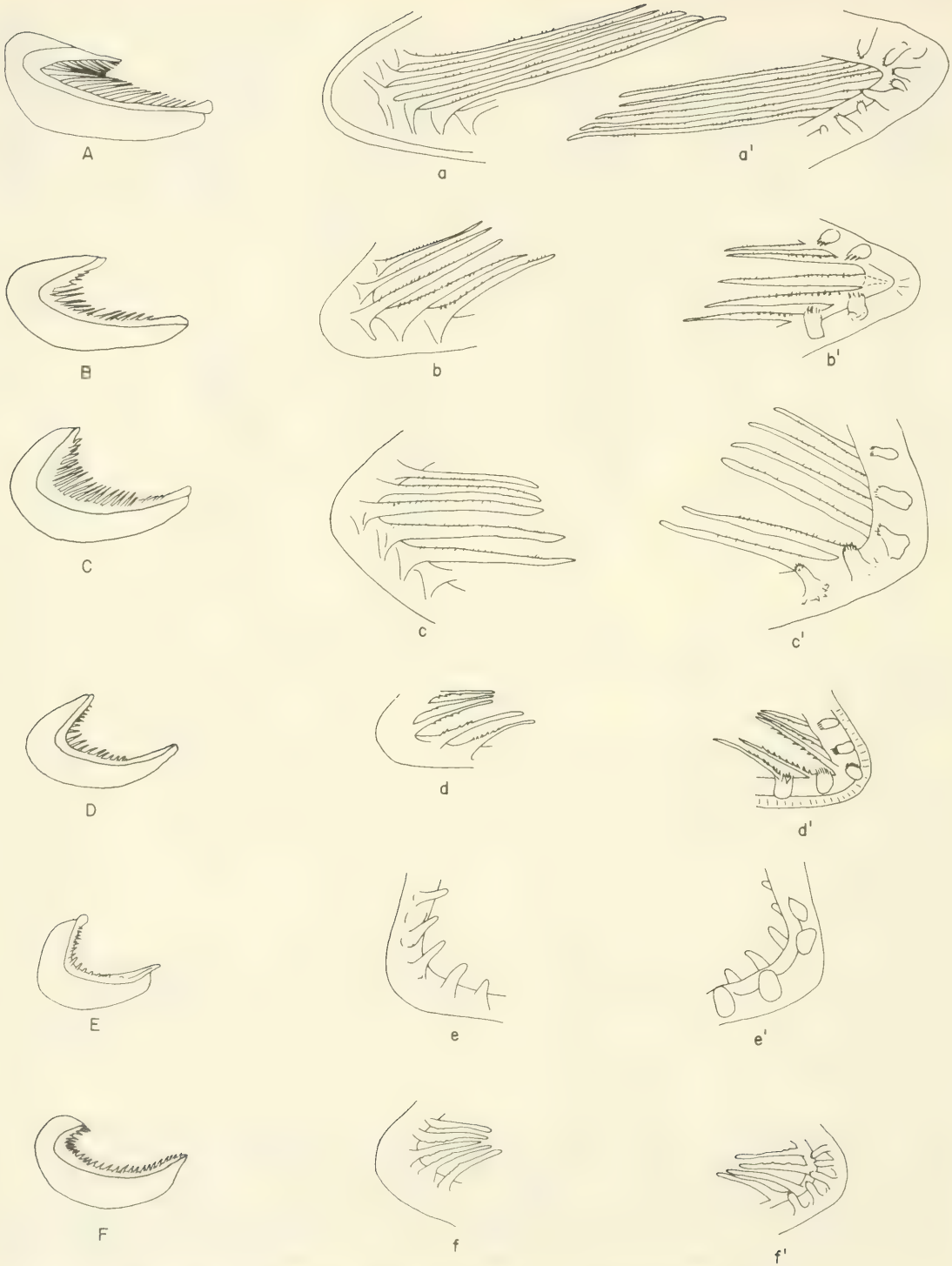


FIGURE 24.—First right gill arch in juveniles of six species of sciaenids: A, a, a′, *Larimus fasciatus*; B, b, b′, *Cynoscion regalis*; C, c, c′, *Bairdiella chrysoura*; D, d, d′, *Micropogonias undulatus*; E, e, e′, *Menticirrhus saxatilis*; F, f, f′, *Leiostomus xanthurus*. a–f, lateral view at the corner, a′–f′, medial view at the corner.

The inner gill rakers are knoblike, sometimes with spicules or teeth on their distal ends (Figure 24a′–f′). *Cynoscion regalis, Micropogonias undulatus,* and *Menticirrhus saxatilis* have broad, short inner gill rakers, with the height not longer than the width of the base. *Cynoscion regalis* and *Micropogonias undulatus* have prominent spicules at the distal ends of their inner gill rakers (Figure 24b′, d′). *Menticirrhus saxatilis* lacks spicules on its inner gill rakers (Figure 24e′). *Larimus fasciatus, B. chrysoura,* and *Leiostomus xanthurus* have long inner gill rakers, with the height longer than the width of the base. *Larimus fasciatus* and *B. chrysoura* have prominent spicules at the distal ends of their inner gill rakers (Figure 24b′, c′). *Leiostomus xanthurus* has minute spicules on its inner gill rakers (Figure 24f′). Furthermore, in *Larimus fasciatus* a small inner gill raker is often present in between the larger inner gill rakers (Figure 24a′). This is rather common among western Atlantic sciaenids (Chao in press).

The lateral and inner gill rakers on the second to fifth gill arches are similar in size and structure to the inner gill rakers on the first gill arch. The gill arches of these six species also differ in the relative lengths of the epibranchial (upper) arm and ceratobranchial (lower) arm (Figure 24). *Leiostomus xanthurus* has the shortest upper arm and *M. saxatilis* has the shortest lower arm. The numbers and size of the gill rakers indicate that midwater feeders have lateral rakers longer than those of bottom feeders. The relative lengths of inner rakers are longer in fishes with higher numbers of lateral rakers, e.g., *Larimus fasciatus* and *Leiostomus xanthurus* (Figure 24a′, f′; Table 6). Although *Micropogonias undulatus* has the strongest spicules on the lateral gill rakers (Figure 24d), the midwater feeders usually have better developed spicules on the lateral rakers than the bottom feeders (Figure 24). Higher numbers of rakers (both inner and lateral) are associated with filter feeding.

Digestive Tract

The digestive tract of sciaenids includes four parts: esophagus, stomach, pyloric caeca, and intestine. The intestine usually has two loops (Figure 25), except that of *C. regalis* which is a straight tube from stomach to anus (Figure 25B). The relative position and size of the stomach and intestine vary with the amount of food present. The numbers of pyloric caeca and the relative length of the intestine may be correlated with feeding habits (Suyehiro 1942). The relative length of the intestine of these six species of sciaenid fishes (Table 7) may be grouped into three general categories. *Cynoscion regalis* has the shortest intestine, less than half the standard length. *Bairdiella chrysoura* has an intermediate intestine length. *Micropogonias undulatus, Menticirrhus saxatilis, Larimus fasciatus,* and *Leiostomus xanthurus* have long intestines. The numbers of pyloric caeca (Table 8) in these six sciaenid fishes show a similar trend. *Cynoscion regalis* has the fewest pyloric caeca, four or five. *Bairdiella chrysoura* and *M. saxatilis* usually have 6 or 7, and *Micropogonias undulatus* and *L. xanthurus* have 7 to 10 pyloric caeca. *Larimus fasciatus* has the most, 10 or 11. *Larimus fasciatus* and *Leiostomus xanthurus* have both a longer intestine and more pyloric caeca, but *Larimus fasciatus* is a midwater feeder and *Leiostomus xanthurus* is a bottom feeder. They both consume large numbers of small crustaceans (see "Food Specialization" section). *Cynoscion regalis* has the shortest intestine and the fewest pyloric caeca. Its diet is mainly composed of large crustaceans and fishes. Thus, the relative lengths of the intestine and the numbers of pyloric caeca in these sciaenids may be correlated with the size of the food rather than the feeding position in the water column.

TABLE 7.—Relative length of intestine in juveniles of six species of sciaenids from the York River.

Species	SL (mm)	Intestine length in % of SL			
		Range	$\bar{x}$	SD	*N*
Cynoscion regalis	35.2-152	35.5-49.6	40.24	3.07	36
Bairdiella chrysoura	30.0-151	46.1-64.1	55.34	5.92	30
Micropogonias undulatus	35.5-145	52.3-88.6	65.57	6.56	39
Menticirrhus saxatilis	29.2-91.2	56.6-88.2	76.06	6.67	26
Larimus fasciatus	35.3-99.8	73.1-97.7	83.87	9.08	14
Leiostomus xanthurus	47.4-166	73.6-97.8	84.69	6.95	30

TABLE 8.—Number of pyloric caeca in juveniles of six species of sciaenids from the York River.

Species (size in mm SL)	4	5	6	7	8	9	10	11	*N*	$\bar{x}$
Cynoscion regalis (35.2-82.4)	20	14							34	4.41
Bairdiella chrysoura (30.0-75.3)			8	20	1				29	6.76
Menticirrhus saxatilis (29.2-99.6)			11	19					30	6.63
Micropogonias undulatus (35.5-116)				1	25	11			37	8.27
Leiostomus xanthurus (47.4-148)				6	13	8	1		28	8.14
Larimus fasciatus (55.3-107)							9	6	15	10.4

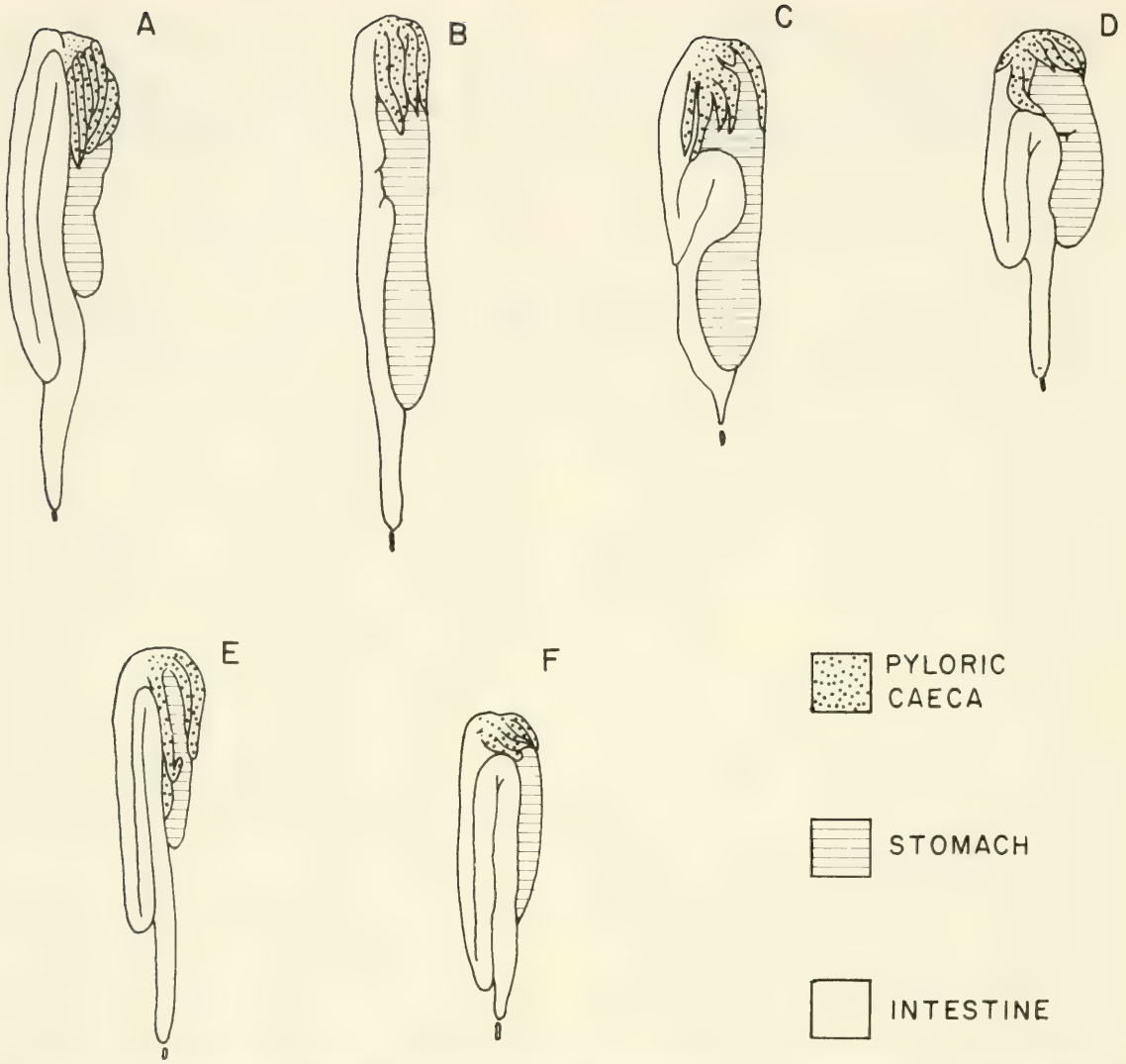


FIGURE 25.—Ventral view of the digestive tract in juveniles of six species of scaienids: A. *Larimus fasciatus*; B. *Cynoscion regalis*; C. *Bairdiella chrysoura*; D. *Micropogonias undulatus*; E. *Menticirrhus saxatilis*; F. *Leiostomus xanthurus*.

Pores and Barbels

The pores on the snout and the tip of the lower jaw, and mental barbels in fishes are sense organs probably involved in touch, taste, or both. The number and arrangement of the pores and barbels in sciaenid fishes are closely related to their feeding habitats (Chao 1976). These six species of sciaenid fishes show a gradual increase in the number and size of pores from upper water column feeders to lower water column and bottom feeders (Figure 26). *Larimus fasciatus* has five marginal pores on the snout and four minute pores at the tip of the underside of the lower jaw (Figure 26A, a). *Cynoscion regalis* has only two marginal pores on the snout and no pores or barbels on the lower jaw (Figure 26B, b). *Bairdiella chrysoura* has five marginal and five upper pores on the snout, and six mental pores at the tip of the lower jaw (Figure 26C, c). *Leiostomus xanthurus* has five marginal and five upper pores on the snout, and five mental pores at the tip of the lower jaw (Figure 26F, f).

Micropogonias undulatus also has five marginal and five upper pores on the snout, and five mental

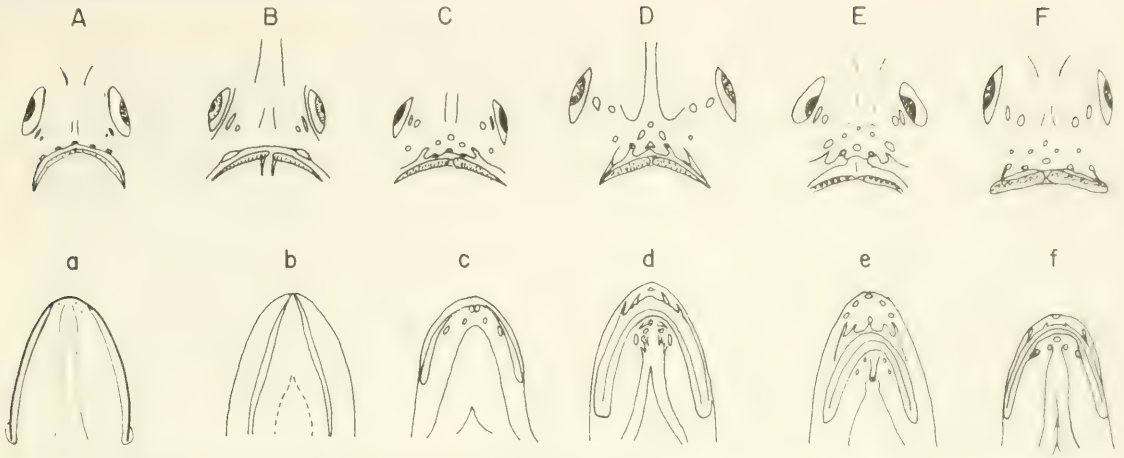


FIGURE 26.—Anterior view of snout (captial letters) and ventral view of lower jaw (lower case letters) in juveniles of six species of sciaenids: A, a, *Larimus fasciatus*; B, b, *Cynoscion regalis*; C, c, *Bairdiella chrysoura*; D, d, *Micropogonias undulatus*; E, e, *Menticirrhus saxatilis*; F, f, *Leiostomus xanthurus*.

pores plus six minute barbels at the tip of the lower jaw (Figure 26D, d). *Menticirrhus saxatilis* has five marginal pores and three upper pores on the snout, and four mental pores and a short, rigid barbel at the tip of the lower jaw (Figure 26E, e). An apical pore is also present on the barbel of *M. saxatilis*. The anterior margin of the snout (rostral fold) in *Larimus fasciatus* and *C. regalis* is complete without notches (Figure 26A, B). *Bairdiella chrysoura* and *Leiostomus xanthurus* have a slightly indented rostral fold (Figure 26C, F), although the former has a terminal mouth and the latter has an inferior mouth (Figure 26c, f). Both *M. saxatilis* and *Micropogonias undulatus* have deeply notched rostral folds (Figure 26D, E), correlated with their inferior mouth positions. The mental pores of *Larimus fasciatus* (Figure 26a) are the smallest of these sciaenids. The barbels of *M. undulatus* and *Menticirrhus saxatilis* may differ in function as well as in number, because the single barbel of *M. saxatilis* has a pore at the tip, whereas barbels of *Micropogonias undulatus* do not (Figure 26d, e). The numbers and size of pores increase from species to species as the feeding niche tends toward the bottom; barbels are present only in the bottom feeders.

Nares

Sciaenid fishes have two pairs of closely set nostrils. The anterior one is usually round; the posterior one is oval and elongate (Figure 27). A flap of skin is sometimes also present along the posterior margin of the anterior nostril in bottom feeding species. The nasal cavity is generally oval shaped with a cluster of olfactory laminae forming a nasal rosette anteriorly. *Larimus fasciatus* has the shortest nasal cavity from anterior to posterior nostril (Figure 27A), and *Leiostomus xanthurus* has the longest (Figure 27F). The shape of the nasal rosettes and olfactory laminae are similar in these six species of sciaenid fishes. The mean number of laminae (averaging both sides per specimen and rounding upwards) differs among these species (Table 9) and is variable within a species. The numbers of laminae are 11 to 14 in *Larimus fasciatus*; 12 to 22 in *C. regalis*; 12 to 25 in *B. chrysoura*; 10 to 31 in *M. undulatus*; 11 to 22 in *Menticirrhus saxatilis*; and 16 to 30 in *Leiostomus xanthurus*. *Larimus fasciatus, C. regalis,* and *B. chrysoura* average fewer laminae than *Micropogonias undulatus, L. xanthurus,* and *Menticirrhus saxatilis* (Table 9). Within a species, the number of nasal laminae seems higher in larger specimens. The maximum number of nasal laminae tends to be greater in bottom feeding fishes.

Other Morphological Characters

Differences in body shape, mouth structure, food specialization, and habitat preferences of fishes may act to restrict interspecific competition within a fauna (Keast and Webb 1966). The six species of sciaenid fishes discussed here show a

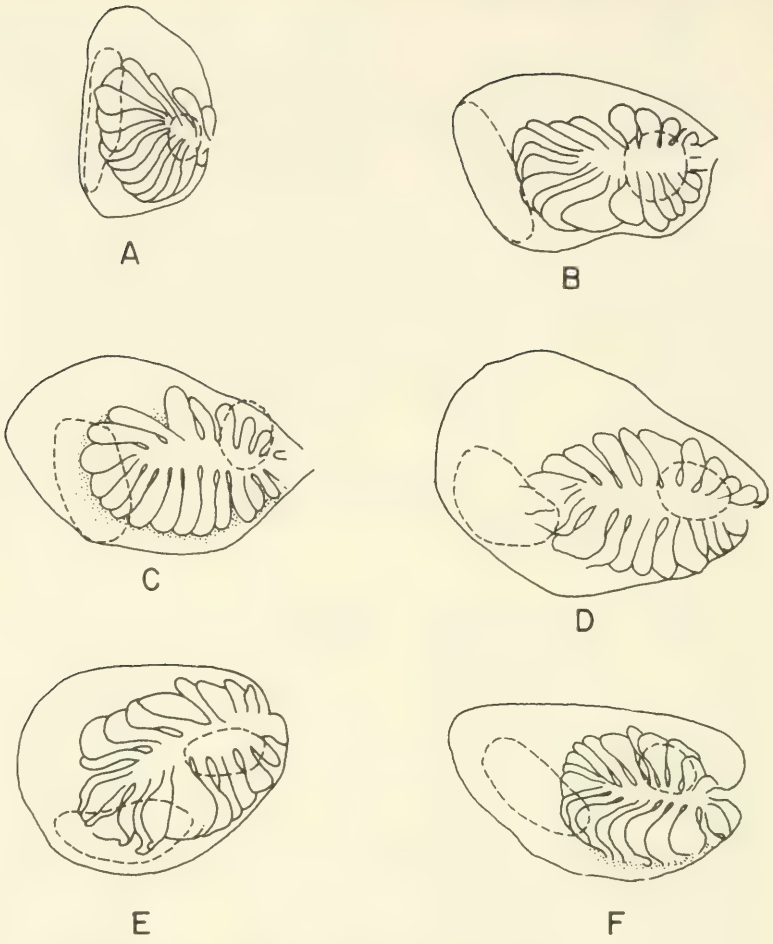


FIGURE 27.—Right olfactory rosette and nasal cavity in juveniles of six species of sciaenids: A. *Larimus fasciatus*; B. *Cynoscion regalis*; C. *Bairdiella chrysoura*; D. *Micropogonias undulatus*; E. *Menticirrhus saxatilis*; F. *Leiostomus xanthurus*. Dotted circles represent nostrils, the anterior nostril to the right.

TABLE 9.—Number of laminae in olfactory rosettes in juveniles of six species of sciaenids from the York River.

Species (size in mm SL)	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	*N*	$\bar{x}$
Larimus fasciatus (55.3-107)		3	5	2	5																		15	12.6
Cynoscion regalis (35.2-86.4)			1	6	6	4	7	5	1	2	1	1	2										36	15.9
Bairdiella chrysoura (30.0-75.3)			2	2	2	8	4	6	2	6	3	—	—	1	—	1							37	16.8
Micropogonias undulatus (35.5-116)	1	1	—	—	3	3	4	3	3	—	2	1	2	3	2	—	2	1	1	1		1	34	19.5
Menticirrhus saxatilis (29.2-99.6)		1	—	—	1	6	6	3	3	6	3	2	1										32	17.3
Leiostomus xanthurus (47.4-148)							1	2	4	4	3	2	7	6	—	1	5	1	—	—	1		37	21.7

correlation between body shape and feeding habitat (Figure 28). Young *Larimus fasciatus* are oblong, relatively deep, and have a compressed body and a double truncate tail (Figure 28A). These features, in combination with a strong oblique mouth and large eyes (Figure 20A, A′; Table 5), indicate that *L. fasciatus* is a moderate swimmer that feeds in the upper water column by sight. Young *C. regalis* have a more fusiform and compressed body, and a long pointed tail (Figure 28B). These features, in combination with a large lique mouth and relatively large eyes (Figure 20B, 20B, B′; Table 5), indicate that *C. regalis* is a fast swimmer that feeds in the upper to middle water column by sight. Young *B. chrysoura* have an oblong and compressed body, and a broad and

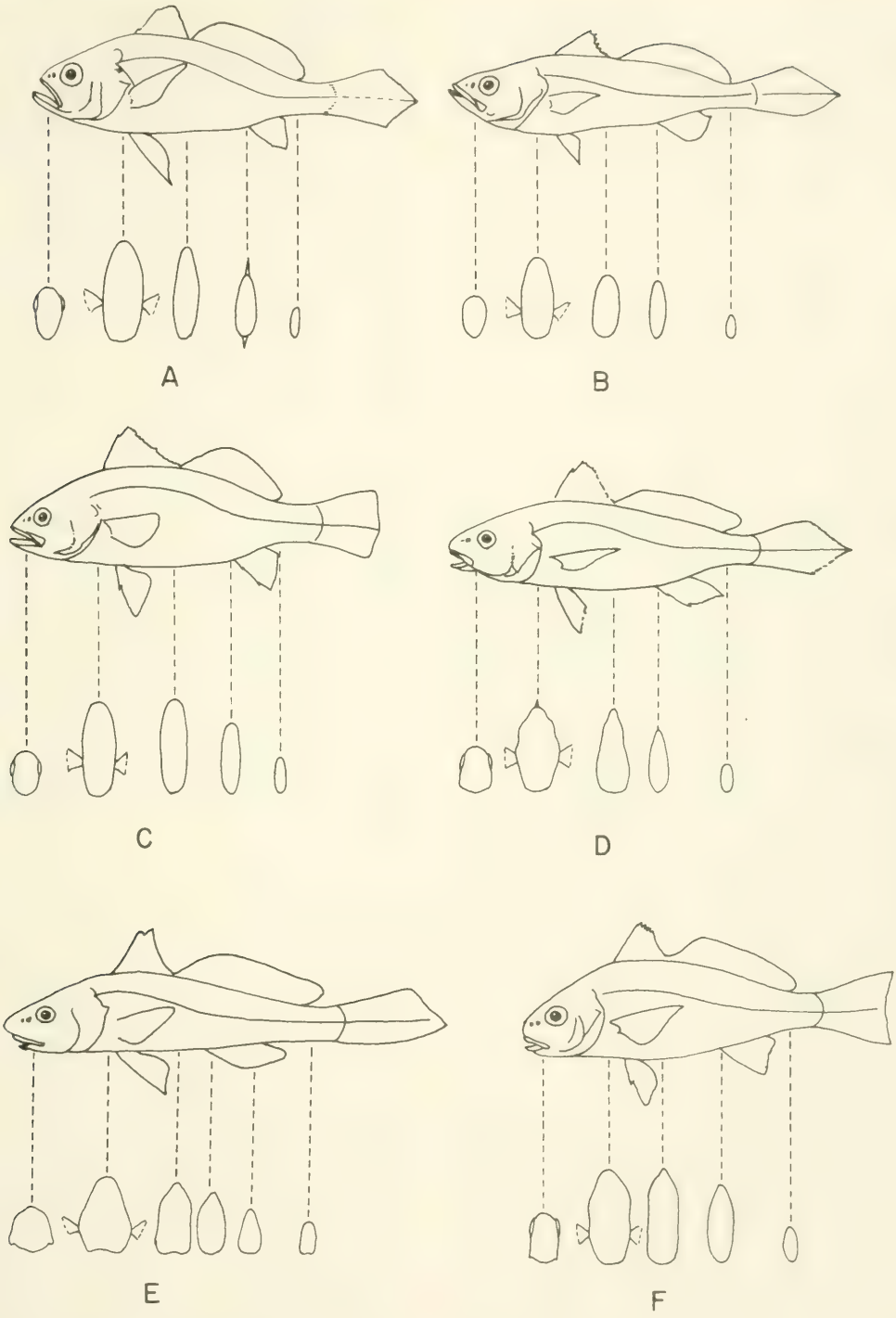


FIGURE 28.—Body shape and cross sections in juveniles of six species of sciaenids: A. *Larimus fasciatus*; B. *Cynoscion regalis*; C. *Bairdiella chrysoura*; D. *Micropogonias undulatus*; E. *Menticirrhus saxatilis*; F. *Leiostomus xanthurus*.

slightly rounded to truncate tail (Figure 28C). These features, together with its terminal mouth and relatively large eyes (Figure 20C, C′; Table 5), indicate that *B. chrysoura* is a moderately fast swimmer that feeds in the middle water column by sight. Young *Micropogonias undulatus* have an elongate and less compressed body and a long pointed tail (Figure 28D). These features, combined with an inferior mouth with barbels and relatively smaller eyes (Figure 20D, D′; Table 5), indicate that *M. undulatus* is a moderately fast swimmer that feeds in the lower water column by sight, olfaction, and touch. Young *Leiostomus xanthurus* have a rather short and deep body, and a broad and truncate tail (Figure 28F). These features, combined with an inferior mouth and large eyes (Figure 20F, F′; Table 5), indicate that *L. xanthurus* is a slow swimmer that feeds in the lower water column by sight and olfaction. Young *Menticirrhus saxatilis* have an elongate, round, and narrow body, and a relatively pointed tail (Figure 28E). These features, combined with an inferior mouth with a pored-barbel (Figure 26e) and relatively smaller eyes (Figure 20E, E′; Table 5), indicate that *M. saxatilis* is a slow swimmer that feeds in the lower water column by olfaction and touch.

The cross sections of these young sciaenid fishes (Figure 28) also reflect their habitat. *Larimus fasciatus*, *C. regalis*, and *B. chrysoura* are compressed and have relatively narrow ventral surfaces (Figure 28A–C) in comparison to *Micropogonias undulatus*, *Leiostomus xanthurus*, and *Menticirrhus saxatilis* (Figure 27D–F). Some of these morphological characters, such as the shape of the tails and the size of the eyes, vary ontogenetically. Generally, most juvenile sciaenids have pointed tails and relatively larger eyes than adults.

Food Specialization

The food habits of young sciaenids have been studied by numerous authors and the information reported by them is scattered and presented in different ways. Some of this work has been summarized for comparison with the present study (Tables 10–14). Only those studies having some sort of quantitative analysis were chosen for the comparison. Different authors have used different taxonomic categories to analyze their information. The classification of the food items in the present study has been modified from Darnell (1961) and Qasim (1972). Six major food groups were employed more or less according to their vertical occurrence in the water column, from the upper water column to the bottom. They were fishes, macrozooplankton, microzooplankton, epibenthos, infauna, and other organic matter. Within each food group, several items were listed and the generic and specific names of the primary prey species in the study area were indicated. Boundaries for these six food groups are not definite because some prey taxa move vertically in the water column and some taxa may also include both pelagic and benthic species. Generalized terms used by many authors such as shrimps, annelids, mollusks, crabs, etc., were placed under respective food groups for the convenience of comparison. Food habits of each species were compared with previous studies from different geographic areas and seasons. Food items were listed in different categories for each species. Under each listed item, there were cases where more than a single food taxon was listed by the original authors. Then, the one that had the highest frequency (by occurrence, volume, or weight) was chosen to represent that item.

All fish specimens used for stomach analyses in this study were randomly selected from specimens collected in June to November (1972 to 1974). During this period, these sciaenids reach their maximum abundance and degree of sympatry. All specimens were young-of-the-year or yearlings.

Larimus fasciatus

Stomachs of 12 *L. fasciatus* (14–125 mm TL) were examined. All stomachs contained crustaceans, exclusively: *Neomysis americana* in seven stomachs, Cumacea in five, Amphipoda (mostly *Gammarus* spp.) in four, and calanoid copepoda (mostly *Acartia tonsa*) in two. Most of these prey species were of small size.

Published information on the food habits of *L. fasciatus* was scarce. Welsh and Breder (1923) reported on food of four *L. fasciatus* (50–110 mm SL) from Mississippi and Texas. Only two stomachs had food, one with a post-larval clupeoid and the other with "schizopodous forms" (crustacean remains).

Cynoscion regalis

Stomachs of 36 *C. regalis* (67–183 mm TL) were examined (Table 10). They fed mostly on *Anchoa mitchilli* and *N. americana*. *Anchoa mitchilli* was very abundant in the same area as *C. regalis* in the

TABLE 10.—Stomach contents of weakfish, *Cynoscion regalis*, from different estuarine areas along U.S. Atlantic coast.

Author	Chao 1976	Welsh and Breder 1923				Merriner 1975	
Locality	York River, Va.	Acushnet River, Mass.	Cape Charles, Va.	Winyah Bay, S.C.	Fernandina, Fla.	Pamlico Sound and Morehead City, N.C.	
Period	June-Aug. 1973	Sept. 1882	Sept. 1916	July 1915	Mar. 1920	June 1967-Jan. 1970	
Source	Original	p. 159	p. 160	p. 161	p. 161	Table 1	
Number of specimens	36	28	45	34	105	2,159	
Empty stomachs	2	5	0	5	74	1,342	
Length of specimens	70-183 mm TL	7-11 cm SL	43-11.5 cm SL	2.8-6.2 cm SL	5-17 cm SL	135-481 mm SL	
Quantitative method	% of occurrence	% of volume	% of volume	% of volume	% of volume	% of occurrence	% of volume
Fishes:							
Anchoa mitchilli	72.2					58.1	15.6
Others and remains	8.3	48.0	2.0	9	18	15.7	74.0
Macrozooplankton:							
Mysidace	2.8						
Neomysis americana	63.9					31.0	0.9
Isopoda		0.5		6			
Decapoda (shrimps)		47.0	0.5		46	0.1	
Others and remains			91.0	83	18	1.5	1.2
Microzooplankton:							
Copepoda			3.5	2			
Epibenthos:							
Polychaeta		0.5				0.5	
Amphipoda			3.0				0.1
Others and remains						1.5	
Unidentified remains	5.6	4.0			18	96.8	8.2

Author	Thomas 1971					Stickney et al. 1975
Locality	Delaware River, Del.					Savannah River and Ossabaw Sound, Ga.
Period	June 1969	July 1969	Aug. 1969	Sept. 1969	Oct. 1969	May 1972-July 1973
Source	Table 20	Table 20	Table 20	Table 20	Table 20	Table 1
Number of specimens	71	94	94	120	66	120
Empty stomachs	10	11	10	18	12	35
Length of specimens	11-76 mm TL	5-123 mm TL	15-180 mm TL	20-180 mm TL	61-180 mm TL	30-169 mm SL
Quantitative method	% of occurrence	% of occurrence	% of occurrence	% of occurrence	% of occurrence	% of occurrence
Fishes	[1]7.0	[1]14.9	[1]16.0	[1]33.3	[1]34.8	
Anchoa mitchilli	1.4	2.1	1.1	3.3	4.5	2.5
Others and remains	2.8	7.4	13.8	12.5	30.3	31.7
Macrozooplankton:						
Mysidace	74.6	59.6	65.8	66.7		0.8
Neomysis americana						55.0
Isopoda		4.3	2.1	1.7		2.5
Decapoda (shrimps)		2.1	3.2	6.7	10.6	2.5
Others and remains						
Microzooplankton:						
Copepoda	19.7	4.3	2.1	3.3		5.0
Calanoid						2.5
Others and remains	9.9	4.3	1.1	0.8	1.5	
Epibenthos:						
Neris succinea						15.0
Amphipoda						2.5
Gammarus sp.	9.9	58.5	58.5	28.3	28.8	1.7
Others and remains						9.2
Unidentified remains						2.5

[1]All fishes combined.

same months (Colvocoresses 1975; Markle 1976). Fishes and planktonic crustaceans were the major food items of *C. regalis* (Table 10). A shift of food habits with growth was noted by Thomas (1971), Merriner (1975), and Stickney et al. (1975). The smaller weakfish fed more on mysid shrimp and the larger weakfish fed more on fishes.

Bairdiella chrysoura

Stomachs of 68 *B. chrysoura* (57–190 mm TL) were examined (Table 11). They fed mainly on *N. americanus* and *A. mitchilli*. In other areas, juvenile *B. chrysoura* fed mainly on crustaceans and fishes (Table 11). Smaller specimens (<40 mm SL) fed mostly on copepods but as they grew they fed more on *N. americanus*, amphipods, and other larger crustaceans. Fishes became more important food items for specimens over 70 mm SL (Thomas 1971; Carr and Adams 1973; Stickney et al. 1975).

Micropogonias undulatus

Stomachs of 69 *M. undulatus* (65–199 mm TL) were examined (Table 12). They showed as wide a variety of prey items as have previous studies from other geographic areas (Table 12). Polychaetes

TABLE 11.—Stomach contents of silver perch, *Bairdiella chrysoura*, from different estuarine areas along U.S. Atlantic and Gulf of Mexico coasts.

Author	Chao 1976	Thomas 1971	Welsh and Breder 1923
Locality	York River, Va.	Delaware River, Del.	Cape Charles, Va.
Period	June-Aug. 1973	Aug.-Oct. 1969	Sept. 1916
Source	Original	Table 46	p. 174-175
Number of specimens	68	99	21
Empty stomachs	10	9	0
Length of specimens	57-153 mm TL	5-130 mm TL	6-8.2 cm TL
Quantitative method	% of occurrence	% of occurrence	% of occurrence
Fishes		[1]12.1	
Anchoa mitchilli	5.1	3.0	
Others and remains	20.7	8.1	1
Macrozooplankton:			
Mysidace	1.7	89.9	
Neomysis americana	74.1		
Isopoda	1.7	1.0	
Decapoda (shrimp)	10.3	17.2	5
Others and remains	1.7		87
Epibenthos:			
Annelida (polychaete)	3.5		2
Neris succinea	3.5		
Cumacea	1.7		
Amphipoda	1.7	15.2	5
Gammarus sp.	3.5	62.6	
Crabs		3.0	
Others and remains	1.7		
Infauna (bivalve and Nematoda)	3.5		
Unidentified remains	6.9	2.0	

Author	Stickney et al. 1975	Reid, 1954		Carr and Adams 1973
Locality	Savannah River and Ossabaw Sound, Ga.	Cedar Key, Fla.		Crystal River, Fla.
Period	May 1972-July 1973	June 1950-May 1951		Oct. 1970-Aug. 1971
Source	Table 1	Table 5		Estimate from Fig. 9
Number of specimens	161	45	6	195
Empty stomachs	48	0	0	43
Length of specimens	30-149 mm TL	25-99 mm SL	100-130 mm SL	5-130 mm TL
Quantitative method	% of occurrence	% of occurrence		% of occurrence
Fishes:				
Anchoa mitchilli	2.7			
Others and remains	6.6	4.4	16.6	31.2
Macrozooplankton:				
Mysidace	0.6			
Neomysis americana	25.1			
Isopoda	1.1			
Decapoda (shrimp)	5.5	73.3	33.3	51.6
Others and remains	8.2	4.4	66.6	
Microzooplankton				
Copepoda	3.9	4.0		
Others and remains	2.2			
Epibenthos:				
Annelida (polychaete)	0.6	2.2		7.3
Neris succinea	8.2			
Amphipoda	2.2	33.3	16.6	9.2
Gammarus sp.	6.0			
Crabs	8.2		16.6	
Others and remains	0.6	6.6		
Unidentified remains				8

[1]All fishes combined.

and crustaceans were the main food items of the juvenile *M. undulatus* in the study area. Juvenile *M. undulatus* fed on a large variety of invertebrates and sometimes fishes (Table 12). Stickney et al. (1975) indicated that smaller specimens (<100 mm SL) depend extensively on harpacticoid copepods, which are mainly bottom dwellers. As the fish grow, they become more generalized feeders (Parker 1971). Geographic variation in food habits of juvenile *M. undulatus* (Table 12) probably is attributable to availability of prey species in the area.

Menticirrhus saxatilis

Stomachs of 20 *M. saxatilis* (36.5–118 mm TL) were examined. All contained crustaceans and polychaetes were also important in their diet. The occurrence of organic detritus was also frequent suggesting that *M. saxatilis* is a bottom feeder. The literature also indicates that juvenile *M. saxatilis* feed mainly on crustaceans and polychaetes (Table 13). Welsh and Breder (1923) indicated that *M. saxatilis* fed mainly on relatively large crustaceans.

Leiostomus xanthurus

Stomachs of 77 *L. xanthurus* (73–205 mm TL) were examined. Although they showed a wide variety of food species, the major part of the food was benthic. *Pectinaria gouldii*, a burrowing polychaete, was a major food item in the diet of *L. xanthurus* in the study area. Stickney et al. (1975)

TABLE 12.—Stomach contents of croaker, *Micropogonias undulatus*, from different estuarine areas along U.S. Atlantic and Gulf of Mexico coasts.

Author	Chao 1976	Thomas 1971	Roelofs 1954	Welsh and Breder 1923		Stickney et al. 1975	Hansen 1969	Parker 1971			
Locality	York River, Va.	Delaware River, Del.	North Carolina coast	Winyah Bay, S.C.	Cape Canaveral, Fla.	Savannah River and Ossabaw Sound, Ga.	Pensacola, Fla.	Lake Pontchartrain, La.		Clear Lake, Tex.	
Period	June-Aug. 1973	Nov.-Dec. 1970	All seasons 1950	July 1915	Dec. 1919	May 1972-July 1973	Aug. 1953-Dec. 1965	Jan. 1963-Dec. 1965			
Source	Original	Table 71	Table 1	p. 184	p. 183	Table 1	Table 5	Table 28			
Number of specimens	69	25	159	37	24	196	2,520	63	44	1,866	475
Empty stomachs	5	3	?	0	6	15	?	2	6	194	15
Length of specimens	56-199 mm TL	23-50 mm TL	60-140 mm TL	4.2-6.2 cm SL		39-180 mm SL	76-173 mm TL	10-74 mm TL	75-124 mm TL	10-96 mm TL	70-110 mm TL
Quantitative method	% of occurrence	% of occurrence	% of occurrence	% of volume		% of occurrence	% of volume	% of occurrence			
Fish and remains	20.3		3.1	0.7		7.5	15.9	11	9	4	5
Macrozooplankton							[1]14.3				
Mysidace	3.1	64.0	5.7			1.0		5	4.5	2	2
Neomysis americana	35.9					16.9					
Isopoda	1.6	4.0				1.0		6.5	8.0	10.5	18.0
Decapoda (shrimp)	9.4		3.1	7.0	24.0	3.0		17.0	18.5	19.5	14.5
Insecta	1.6					0.5		3	18.5	13.0	20.0
Others and remains	3.1			7.0							
Microzooplankton:											
Copepoda	3.1	76.0	25.2			7.0		2.0	6.5	1.0	3.0
Calanoid	10.9					1.0					
Harpacticoid						10.0					
Ostracoda						0.5		8.0	12.0	9.0	8.0
Others and remains	6.3		4.4	2.0							
Epibenthos:											
Annelids											
(polychaetes)	67.2		89.9	29.0	3.0	12.4	61.5	17.0	6.5	6.0	7.0
Neris succinea	18.8					3.0					
Glycinde solitaria	9.4										
Phyllodocid	1.6										
Spionid	6.3					1.0					
Cumacea	4.7			2.0		6.0		4.0	4.5	5.0	16.0
Amphipoda	21.9		5.7			8.0					
Gamanarus sp.	7.9					9.5		17.0	10.0	16.0	10.5
Crabs	3.1			1.8		4.5		17.0	18.5	22.0	18.0
Others and remains	6.3			1.0	2.5	7.0					
Infauna:											
Pectinaria gouldii	15.6										
Ampharetid	1.6										
Gastropoda	1.6							[2]9.0	[2]3.0	[2]18.0	[2]18.0
Pelecypoda			11.3			2.5	[2]3.5				
Nematoda			0.6				0.3				
Unidentified remains and organic matters	23.5		4.4	22.0	48.0	35.6	2.5	17.0	14.0	12.0	9.0

[1]Arthropods.
[2]Mollusks.

TABLE 13.—Stomach contents of northern kingfish, *Menticirrhus saxatilis*, from different estuarine areas along U.S. Atlantic coast.

Author	Chao 1976	Welsh and Breder 1923	
Locality	York River, Va.	Cape May, N.J.	Falmouth, Mass.
Period	Mar. 1972-Dec. 1974	Aug. 1916	Aug. 1892
Source	Original	p. 194	p. 194
Number of specimens	20	21	17
Empty stomachs	0	0	4
Length of specimens	37-118 mm TL	1.9-7.2 cm SL	2.4-7.4 cm SL
Quantitative methods	% of occurrence	% of vol.	% of vol.
Macrozooplankton:			
Neomysis americana	35.0		
Isopoda		5.0	
Decapoda (shrimp)		9.0	42.0
Crangon septemspinosa	5.0		
Palaemonetes	10.0		
Insecta	5.0		
Others and remains	70.0	9.0	42.0
Microzooplankton:			
Copepoda	5.0		
Calanoid	5.0		
Epibenthos:			
Polychaetes	70.0	19.0	
Glycindae solitaria	10.0		
Spionids	15.0		
Amphipoda	35.0	30.0	
Gammarus sp.	15.0		
Others and remains	40.0		
Unidentified remains and organic matters	50.0	26.0	16.0

found that harpacticoid copepods were the main food for juvenile *L. xanthurus* and that seasonal variations in diet were slight. Organic detritus and unidentified remains were also common in stomachs (Table 14).

Food Partition

To compare the feeding habits of the juveniles of the six sciaenid species, a chart (Figure 29) has been prepared for the six food groups defined previously. The main food group of *Larimus fasciatus* was mostly planktonic and the primary food species was *Neomysis americana*. *Cynoscion regalis* and *B. chrysoura* fed mainly on fishes and macrozooplankton; the primary food species were *Anchoa mitchilli* and *N. americana*, respectively. *Micropogonias undulatus* fed on a wide variety of food including all six food groups, with the dominant food organisms being *N. americana* and *Nereis succinea*. *Menticirrhus saxatilis* fed mainly on macrozooplankton and epibenthos, with the primary food organisms being *N. americana* and polychaetes. *Leiostomus xanthurus* fed on a wide variety of food including five food groups. The dominant food organisms were *Pectinaria gouldii* and other polychaetes.

Neomysis americana was very abundant and available to all species of sciaenids in the study area. This shrimp migrates vertically in response to change in ambient light (Herman 1962). *Neomysis americana* is negatively phototactic. In shallow turbid water (as in the study area) during daylight it might concentrate near the bottom in the darkest sector of the vertical light gradient (Stickney et al. 1975). Because of the abundance and availability of *N. americana*, the other prey items should provide a better indication of feeding specialization. As has been repeatedly shown (Tables 10–14), most fishes were sufficiently opportunistic in their food habits to take advantage of extremely abundant prey species. All the fishes in the present study were sampled by bottom trawl during the daytime. Therefore, both prey and predators probably were dwelling close to the bottom.

Polychaetes were a major food resource for the bottom feeders (Tables 12–14), *Micropogonias undulatus*, *L. xanthurus*, and *Menticirrhus saxatilis*. But *Micropogonias undulatus* fed more on the "crawling" species of worms (Table 12) such as *Nereis* and *Nephthys* (Barnes 1968) and *L. xanthurus* fed more on "tubiculous" or "burrowing" species of worms (Table 14), such as *Pectinaria* and *Amphitrite*. This is contradictory to the findings of Roelofs (1954) and Stickney et al. (1975). Observations of the feeding behavior of these two species in aquarium generally agreed with Roelofs (1954). But *L. xanthurus* seemed to "dive" into the bottom sand much more often than *M. undulatus*, and the depth of the dives by *L. xanthurus* was not shallower than *M. undulatus* as stated by Roelofs (1954).

Correlation of Feeding Structures and Food Habits

Larimus fasciatus and *C. regalis* have oblique mouths (Figure 20A, B) and their upper jaws are slightly or not protrusible (Figure 21A, B). These features allow them to feed anteriorly and dorsally to the longitudinal axis of their bodies along their swimming course. Their mouths open as the lower jaws drop anteroventrally and the distal ends of the premaxillae move forward (Figure 20A′, B′). The mouth openings of *L. fasciatus* and *C. regalis* are relatively larger than in the other species studied (Table 5). The anterior views of their mouths (Figure 20a, a′, b, b′) show that the upper jaws (premaxillae) are longer or equal to the lower jaws (dentaries). Although both of them feed "anterodorsally" and pelagically, they did show differences in diet (Figure 29). The following mor-

TABLE 14.—Stomach contents of spot, *Leiostomus xanthurus*, from different estuarine areas along U.S. Atlantic and Gulf of Mexico coasts.

Author	Chao 1976	Roelofs 1954	Stickney et al. 1975	Welsh and Breder 1923	Townsend 1956	Parker 1971	
Locality	York River, Va.	North Carolina	Savannah River and Ossabaw Sound, Ga.	St. Vincent Sound, Fla.	Alligator Harbor, Fla.	Lake Pontchartrain, La.	Clear Lake, Tex
Period	June-Aug. 1973	All seasons 1950?	May 1972-July 1973	Apr. 1915	June 1955-May 1956	July 1959-Mar. 1961	
Source	Original	Table 1	Table 1	p. 179	Table 3	Table 13	
Number of specimens	77	73	126	50	45	22	457
Empty stomachs	4	0	7	0	9	4	60
Length of specimens	73-202 mm TL	60-140 mm TL	50-149 mm SL	2.1-3.5 cm SL	16-163 mm SL	40-99 mm TL	18-99 mm TL
Quantitative method	% of occurrence	% of occurrence	% of occurrence	% of volume	% of occurrence	% of occurrence	
Fish & remains	8.2	6.8	5.0		11.1	19	14
Macrozooplankton:							
Mysidace	8.2	4.1				14.5	8.5
Neomysis americana	27.4	7.4					
Isopoda	2.7					7.0	16.0
Decapoda (shrimp)	1.4	5.5	0.8		5.5	19.0	15.0
Insecta	2.7	1.4	1.7			14.0	19.0
Others and remains	1.4		0.8				
Microzooplankton:							
Copepoda	21.9	100		8.0	66.7	3.0	1.0
Cyclopoid	19.2						
Calanoid	13.7		33.1				
Harpacticoid	20.5		88.4				
Ostracoda		2.7	5.8	72.0	2.8	5.0	3.0
Others and remains	1.4	6.8	7.4	1.0		14.5	13.0
Epibenthos:							
Annelids (polychaete)	56.6	32.9	11.6	1.0		14.5	13.0
Neris succinea	27.4		9.1				
Glycinde solitaria	37.0						
Nephthys sp	11.0						
Phyllodocid	6.8						
Spionid	6.8						
Oligochaete	4.1		1.7				
Cumacea	21.9		13.2				
Amphipoda	24.7			2.0		7.0	8.5
Gammarus sp	12.3		11.6		16.7		
Crabs	1.4						
Cnidaria	9.6						
Others and remains	5.5	13.7	2.5	0.5	16.6	19.0	12.0
Infauna							
Pectinaria gouldii	53.4						
Ampharetid	19.2						
Gastropoda	20.5		0.8			4.0	17.0
Pelecypoda	27.4	11.0				1.5	10.0
Nematoda	34.2	71.2			30.6		
Others and remains	5.5		5.0				
Unidentified remains and organic matters	42.5	23.3	35.6	14.0	36.1	14.5	7.0

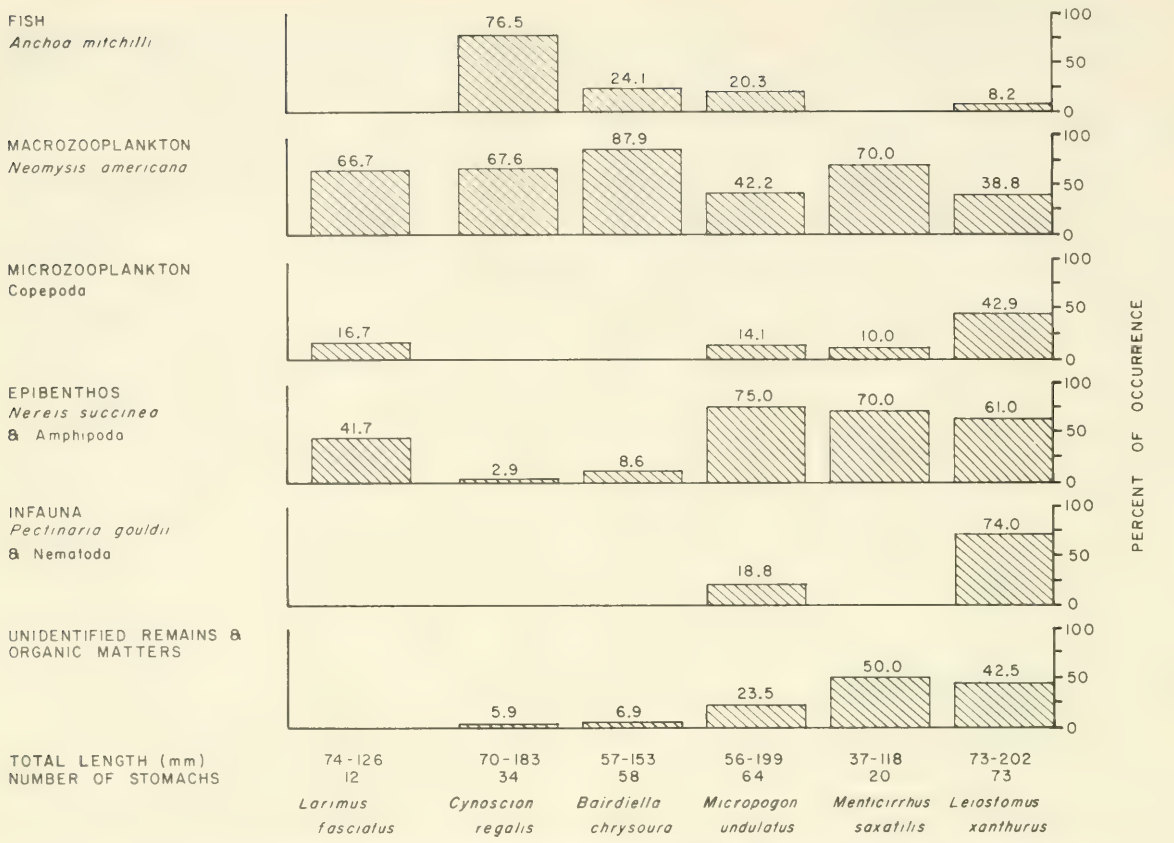


FIGURE 29.—Frequencies of occurence of various categories of food groups in stomachs of juveniles of six species of sciaenids from the York River and lower Chesapeake Bay estuary.

phological characters are correlated with the dietary differences. The premaxillary and dentary teeth of both species are sharp and set in narrow ridges or bands (Figure 22A, B). *Cynoscion regalis* has much larger teeth than *L. fasciatus*, especially a pair of large canines at the tip of upper jaw in *C. regalis*. These large sharp teeth are adaptations for grasping larger swimming prey. Both species have small sharp pharyngeal teeth (Figure 23A, B). The arrangement and size of the gill rakers (Figure 24A, B) in *L. fasciatus* are much denser and longer than those of *C. regalis*. These differences reflect the food contents in the stomachs of *L. fasciatus*, which consisted of small crustaceans collected by filtering. The stomach contents of *C. regalis* consisted of large crustaceans and fishes (Table 10). *Larimus fasciatus* has a much longer two-looped intestine than the straight intestine of *C. regalis* (Figure 25A, B; Table 7). The number of pyloric caeca in *L. fasciatus* (10 or 11) is also higher than in *C. regalis* (4 or 5). These morphological differences are probably correlated with the size of food ingested. The cephalic pore systems of *C. regalis* and *L. fasciatus* are not well developed. *Cynoscion regalis* has only two marginal pores on the snout (Figure 26B) whereas *L. fasciatus* has five minute marginal pores on the snout and four pores on the underside of the lower jaw (Figure 26A). In addition, the more fusiform *C. regalis* (Figure 28B) is adapted for fast swimming and active predation. The robust, and presumably slower moving, *L. fasciatus* (Figure 28A) shows adaptations characteristic of a plankton grazing type of feeding.

Bairdiella chrysoura has a slightly oblique terminal mouth (Figure 20C) and a slightly protrusible upper jaw (Figure 20C'). These features allow the fish to feed directly in front of its body axis along its swimming course. Its mouth opens as the lower jaw drops anteroventrally and the premaxil-

lae move forward (Figure 20C′). The relative size of the mouth opening in *B. chrysoura* (Table 5) is similar to *C. regalis*. The anterior view of its mouth opening shows equal upper and lower jaws (Figure 20c, c′). Although *B. chrysoura* feeds anteriorly, a pelagic feeder, its stomach contents are similar to those of *C. regalis* (Figure 29), except for a smaller proportion of fishes. The jaw teeth of *B. chrysoura* are strong, conical, and arranged in narrow bands, but canines are absent at the tip of the premaxilla (Figure 22C). Its pharyngeal teeth are relatively stronger and blunter than in *C. regalis* (Figure 23B, C), especially along the median rows. Gill rakers of *B. chrysoura* are intermediate between *L. fasciatus* and *C. regalis* in number (Table 6) and length (Figure 24A–C). The intestine of *B. chrysoura* has two loops and its relative length and number of pyloric caeca (6–8) are also intermediate between *L. fasciatus* and *C. regalis* (Figure 25C; Tables 7, 8). These intermediate features reflect the intermediate feeding habits of *B. chrysoura* (Figure 29). In addition, the body shape of *B. chrysoura* is oblong (Figure 28C) and not fusiform as in *C. regalis*, thus resulting in slower swimming and less efficiency in capturing fishes, as reflected in the diet. The relatively well-developed cephalic pore systems of *B. chrysoura* (Figure 26C), three upper and five marginal pores on the snout and six mental pores on the tip of the lower jaw, also may indicate that *B. chrysoura* depends more on "taste" feeding lower in the water column than *L. fasciatus* and *C. regalis*.

Micropogonias undulatus, Leiostomus xanthurus, and *Menticirrhus saxatilis* have inferior mouths (Figure 20D–F) and rather protrusible premaxillae (Figure 21D–F). These features enable them to feed anteriorly and ventrally to their body axis along their swimming courses. Their mouths open as the lower jaws drop ventrally backward and the premaxillae protrude anteroventrally (Figure 20D′–F′). Their mouths are relatively smaller than those of the pelagic feeders described previously (Table 5). The anterior views of their mouths (Figure 20d, d′, e, e′, f, f′) show that the upper jaws (premaxillae) are shorter or equal to the lower jaws (dentaries). Although they all feed anteroventrally and benthically, there are differences in their feeding habits (Figure 29). These differences are reflected in the structural differences in the feeding apparatus and feeding behavior among them. The jaw teeth of *M. saxatilis, Micropogonias undulatus,* and *L. xanthurus* are all set in bands and the outer row of teeth on the upper jaws and an inner row of teeth on the lower jaws are slightly enlarged (Figure 22D–F). The pharyngeal teeth of *M. undulatus* and *Menticirrhus saxatilis* are conical (Figure 23D, E) and the median rows are larger and blunt. *Leiostomus xanthurus* has smaller pharyngeal teeth and the median ones are molariform (Figure 23F). The gill rakers of these three bottom feeding sciaenids differ in number (Table 6) and size (Figure 24D–F). *Menticirrhus saxatilis* has the fewest and shortest gill rakers among them. *Micropogonias undulatus* has fewer but longer gill rakers than *L. xanthurus*. The inner gill rakers of *L. xanthurus* are longest (Figure 24f′) and most numerous (Table 6). This is reflected in the larger numbers of small crustaceans (e.g., copepods) ingested by *L. xanthurus* (Table 14). The relative length of intestines (Table 7) and their in situ position (Figure 25D—F) are similar among these benthic feeders. The average relative intestinal length of *M. undulatus* and *Menticirrhus saxatilis* is slightly shorter than in *L. xanthurus* (Table 7). The numbers of pyloric caeca of these bottom feeders are similar (Table 8). The cephalic pore and barbel system differ among *Micropogonias undulatus, L. xanthurus,* and *Menticirrhus saxatilis*. They all have five upper and five marginal pores on the tip of snout (Figure 26D–F). *Micropogonias undulatus* and *Menticirrhus saxatilis* also have a deeply notched rostral fold. Ventrally, *Micropogonias undulatus* has five pores and six miniature barbels (Figure 26d); *Menticirrhus saxatilis* has four pores and a short rigid barbel with an apical pore (Figure 26e); *L. xanthurus* has five pores and no barbel (Figure 26f). *Menticirrhus saxatilis* also has the most pronounced snout and most elongate and rounded body form (Figure 28E). *Leiostomus xanthurus* has the least pronounced snout and shortest and deepest body form (Figure 28F). *Micropogonias undulatus* is intermediate in snout and body form between *Menticirrhus saxatilis* and *L. xanthurus*.

The length of snout and body form reflect the feeding habits of these three species. Food habits (Figure 29) indicate that *M. saxatilis* and *Micropogonias undulatus* feed on the substrate, on the epifauna, more than they feed "into" the substrate on the infauna. *Leiostomus xanthurus* feeds more on the infauna. The long projecting snout seems to be an obstacle for fishes with an inferior mouth to forage into the bottom for food. Roelofs' (1954) observations on feeding behavior of *M. undulatus* and *L. xanthurus* in aquaria with sandy bottoms were repeated during the present study. Juveniles

of both species foraged into the bottom sand often, especially when the substrate was freshly dug from the beach. Foraging tapered off gradually, especially in *M. undulatus*, apparently as the food in the substrate decreased. Brine shrimp, *Artemia*, were fed to these two species in the aquarium. Both *M. undulatus* and *L. xanthurus* were able to feed on brine shrimp just below the water surface. *Micropogonias undulatus* fed on the surface shrimp in an oblique to vertical position. To feed on brine shrimp close to the surface, *L. xanthurus* occasionally maneuvered in an oblique upside-down position, with the dorsal fin pointing toward the bottom to overcome the inferior position of its mouth.

Other accessory organs of feeding, such as the nares and eyes, also reflect the feeding habits of young sciaenid fishes. The numbers of nasal laminae of the six species (Table 9) overlap, partly due to ontogenetic changes; the absolute numbers of nasal laminae increase as the fishes grow larger. Generally, the bottom feeders, *M. undulatus* and *L. xanthurus*, have more nasal laminae than *Larimus fasciatus, C. regalis,* and *B. chrysoura* (Table 9). *Menticirrhus saxatilis* has relatively fewer nasal laminae than other benthic feeders, but it has a pored mental barbel on the lower jaw. This suggests that *M. saxatilis* depends more on touch for foraging than other benthic feeders. The relative eye size of *M. saxatilis* is smaller than in other sciaenid fishes studied here (Table 5). Larger eyes were found among the pelagic feeders, *L. fasciatus, C. regalis,* and *B. chrysoura* (Table 5). Allometrically, the relative eye size of all these sciaenid fishes is larger in young specimens and smaller in adults. For benthic feeders, decrease in relative eye size with growth is faster than for the pelagic feeders. The relative roles of olfaction, touch, and vision in feeding in young sciaenids studied may be hypothesized as follows. The benthic feeders, *Micropogonias undulatus, L. xanthurus,* and *Menticirrhus saxatilis*, depend more on their senses of smell or touch or both to locate their prey. The pelagic feeders, *Larimus fasciatus, C. regalis,* and *B. chrysoura,* depend more on sight to catch their prey, especially *C. regalis* and *B. chrysoura* which prey on *Anchoa mitchilli*, an active small anchovy.

Morphological differences in the feeding apparatus, especially the mouth position, size, and protrusibility, the form of teeth, and the gill raker structure are limiting factors for the level of water column and the size of the prey species which can be eaten by the fish. The pelagic feeders, *L. fasciatus, C. regalis,* and *B. chrysoura*, almost completely lack any sedentary benthos in their diets (Figure 29). Even among the bottom feeders, *Micropogonias undulatus* feeds more on epibenthic polychaete species (Table 12) and *Leiostomus xanthurus* feeds more on burrowing polychaete species (Table 14).

Morphological differences in the digestive tract, the number of pyloric caeca, and the length of intestine may be adaptations to more efficient use of food. As is evident in *Larimus fasciatus* and *Leiostomus xanthurus*, size of the food items is important; *Larimus fasciatus* fed exclusively on small crustaceans (small Mysidacea and Amphipoda), *Leiostomus xanthurus* fed mainly on copepods (Table 14). *Larimus fasciatus* is mainly a pelagic feeder and *Leiostomus xanthurus* is mainly a benthic feeder. Both species have longer intestines (Table 7) and more pyloric caeca (Table 8) than other species in their respective groups (pelagic and benthic).

Svetovidov reported a similar relationship between the number of gill rakers and size of food items in Caspian shads (Nikolsky 1963). However, he also found more pyloric caeca in shad that fed on fishes than in species that ate small crustaceans, a relationship opposite to that found here. In feeding, the role of gill rakers is in ingestion and the role of the pyloric caeca is in digestion. Although there are morphological and numerical correlations among the ingestive apparatuses and digestive organs, they are highly adaptive and may be variable among fishes.

The so-called "selective feeding habits" of these young sciaenids reported by many previous authors (see citations of Tables 10–14) are not evident in the present study. Partitioning of food among these young sciaenids depends more on the habits of the prey species than on "selective preferences" of the fishes. Juvenile sciaenids feed opportunistically in a limited depth range in the water column, probably within or close to 2 m above the bottom. Within this layer of the water column, *Larimus fasciatus, C. regalis,* and *B. chrysoura* feed in the upper portion of the water column and *M. undulatus, Leiostomus xanthurus,* and *Menticirrhus saxatilis* feed in the lower portion of the water column to the bottom. Feeding niche division and resulting dietary differences among these species of sciaenids in the Chesapeake estuary area are probably attributable to differences in feeding behavior imposed

upon these species by adaptive morphological limitations rather than to selective feeding per se.

CONCLUSION

In the Sciaenidae, a family of primarily coastal marine fishes, many species utilize the same coastal area as common nursery and seasonal feeding grounds. In the York River estuarine system, the coexistence of sciaenid fishes may be attributed to: 1) Differences in their temporal and spatial distributions. Juveniles of the four most abundant sciaenid fishes entered the estuary at different times of the year. Within a given period, the highest catches of each species were usually in different areas (upper and lower reaches) and depths (beach zone, shoals, and channel) of the York River system. Also, the size distributions of each species were often separated temporally and spatially. 2) Differences in their habitat adaptations and food habits. The diverse morphological features of these sciaenid fishes enable them to utilize food resources from different levels (microhabitats) of the water column. Correlations of feeding apparatus, digestive system, and food habits are evident and result in niche division. 3) The abundant food resources of the study area. At times some prey organism (e.g., *Neomysis americanus*) may be ubiquitous and very abundant, providing food for several species of juvenile sciaenids. Then food would not be a limiting resource and intrafamilial competition may not occur.

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THE UNITED STATES SHRIMP FISHERY OFF NORTHEASTERN SOUTH AMERICA (1972–74)[1]

ALBERT C. JONES AND ALEXANDER DRAGOVICH[2]

ABSTRACT

The Guianas–Brazil shrimp fishery off the northeastern coast of South America is supported by four principal species—pink-spotted shrimp, *Penaeus brasiliensis;* brown shrimp, *P. subtilis;* pink shrimp, *P. notialis;* and white shrimp, *P. schmitti*. The areas off Guyana, Surinam, and western French Guiana were dominated by pink-spotted shrimp; brown shrimp were most prevalent off eastern French Guiana and Brazil, pink shrimp off Guyana, and white shrimp off Guyana, French Guiana, and Brazil, chiefly in shallow waters.

U.S.-flag vessels landed 5.0 million pounds of shrimp during the second half of 1972, 13.6 million pounds in 1973, and 9.0 million pounds in 1974. In 1973 and 1974 U.S.-flag vessels took 50% and 39% of the total international landings. Mean annual catch rates for 1972, 1973, and 1974 were 20.0, 26.0, and 18.3 lb/h, respectively. Monthly catch rates peaked each year in March and April and declined gradually thereafter. The catch rates off Brazil were higher than off the Guianas. Most fishing was carried on at night and at depths of 21–35 fathoms.

Small shrimp appeared to be recruited to the fishery mainly in April and October and mainly off French Guiana, Brazil, and Guyana.

An exponential surplus yield model estimated the maximum sustainable yield to be 28.7 million pounds and a linear model estimated the maximum sustainable yield to be 27.1 million pounds. Maximum observed yield was 27.3 million pounds (1973).

The shrimp resource off the northeastern coast of South America (Figure 1) is the basis of a major international fishery. This fishery consists of four principal species—pink-spotted shrimp, *Penaeus brasiliensis;* brown shrimp, *P. subtilis;* pink shrimp, *P. notialis;* and white shrimp, *P. schmitti*. *Penaeus subtilis* and *P. notialis* until recently were known as *P. aztecus subtilis* and *P. duorarum notialis,* respectively (Pérez Farfante in press). The earliest exploratory fishery survey of the continental shelf off the northeastern coast of South America was made in 1944 by Whiteleather and Brown (1945). Commercial shrimp fishing by U.S. vessels began in 1959 stimulated by exploratory surveys made in 1957 and 1958 (Higman 1959; Bullis and Thompson 1959). Thereafter the fishery expanded rapidly and soon included vessels of other nations. The history of the fishery through 1959, and a description of the fishing grounds, species, fishing fleets, and stock status, is given by Naidu and Boerema (1972).

This report is based on data collected in 1972–74 from U.S.-flag vessels and from processing plants under the terms of the bilateral United States–Brazil Shrimp Agreement. This paper evaluates and reviews the status of the fishery based on analysis of these data. Information from processing plant records before 1972 is also used.

The United States–Brazil Shrimp Agreement of 1972 dealt with conservation of shrimp resources and operations of U.S. shrimp vessels off northern Brazil (Allen 1973). The agreement stated that the information on catch and effort, and biological data relating to the shrimp fishery in that area, be collected from U.S. vessels. Similar agreements were effected between Brazil and Barbados, Surinam, and Trinidad and Tobago.

SOURCES OF DATA AND METHODS

Catch data for U.S. vessels came from logbooks and landing records for July 1972–December 1974 (Figure 2; Appendix Table 1). Logbook records were submitted for approximately 50% of the fishing trips, but this percentage varied monthly from 10% at the beginning of data collection to 80% later in the period. Landing records were submitted for all trips. Information on area of cap-

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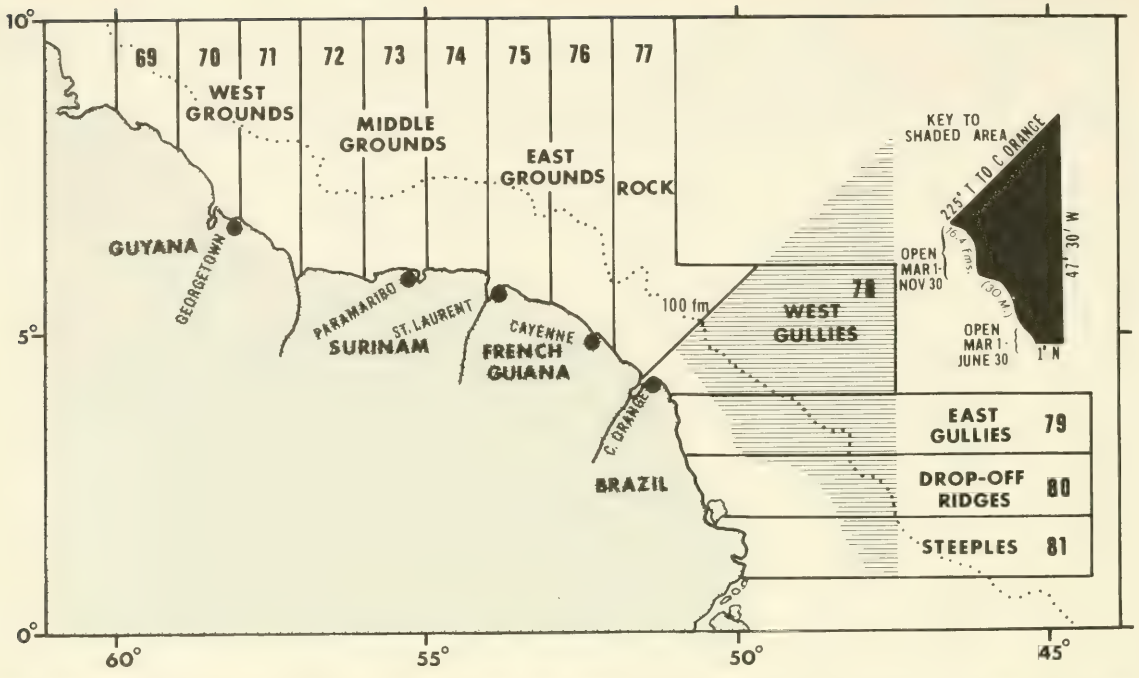

FIGURE 1.—The Guianas–Brazil shrimping grounds. The chart shows the fishing zones and their common names. The United States-Brazil Shrimp Agreement Area is shaded and the boundaries of the Area and the fishing seasons for U.S. vessels are shown in the insert.

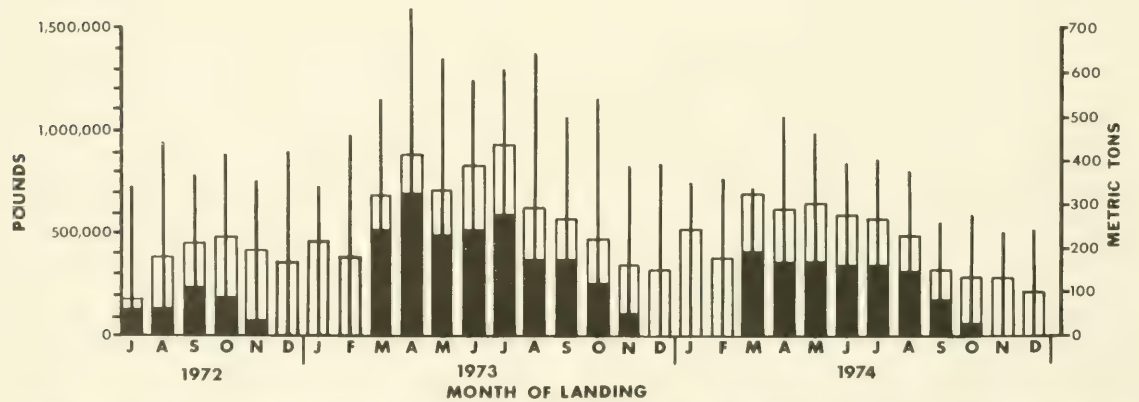

FIGURE 2.—Shrimp catches of U.S. vessels by month and area for the Guianas–Brazil fishery. Weights of heads-off shrimp are in pounds and metric tons. Vertical lines represent the total U.S. landings reported by the processing plants and are reported by month in which the landing was made. Vertical bars represent the "hail" or estimated catches of U.S. vessels submitting logbooks and are reported by the month of capture. The shaded area of the vertical bar represents the proportion of the logged catches recorded from the United States-Brazil Shrimp Agreement Area.

ture, fishing effort, catch, and species and size of shrimp, were taken from logbooks and landing records. The vessel captain made daily entries in the logbook on fishing area (identified by 1°-coastal zone and by water depth), fishing effort (number of hauls and number of hours fishing, by day and by night), estimated shrimp catch (pounds, heads-off weight), and most abundant

species, and commercial tail-weight. The retained catch was reported; no estimate was made of the discarded catch. Landing records for each fishing trip included the total weight of shrimp in each commercial weight category. The landings were recorded in two categories: "mixed" shrimp (pink-spotted, brown, and pink) and white shrimp. In our treatment of the landing data, however, we combined the landings of "mixed" and white shrimp. Information on area of catch was not available in the landing records. In addition, processing plants reported total yearly landings of shrimp and average fleet sizes, including both U.S.- and other-flag vessels.

We estimated total monthly areal catches by adjusting the monthly catches reported by area in logbooks for 1) catches unreported by area and 2) landings unreported in logbooks. For example, the total U.S. catch off northern Brazil (fishing zones 78–81) in April 1974 was estimated as follows:

$$A = A' \times \frac{B}{B'} \times \frac{C}{C'},$$

where A = estimated total catch in zones 78–81, April 1974;

A' = catch reported in logbooks for zones 78–81, April 1974;

B = total catch reported in logbooks, April 1974;

B' = total catch reported in logbooks by fishing zone, April 1974;

C = total landings reported in landing records, April and May 1974;

C' = total catch reported in logbooks, April and May 1974.

The ratio B/B' adjusted A' for the logbook catch that was unreported by fishing zone and the ratio C/C' adjusted for the landings that were unreported in logbooks. The second ratio used data for 2 mo, since catches made in a given month often were landed in both that and the following month. This method resulted in estimates of the total annual catches by areas of capture which were within 2% of the total reported annual landings. The logbook sample was not random and the catch off Brazil was probably overestimated, since more vessels probably submitted information when fishing off Brazil than when fishing off the Guianas. However, there was no way to assess the difference in completeness of reporting of vessels fishing different areas. For this reason, estimates of catches were not made for smaller subareas.

The size index was a weighted mean value calculated by assigning the values 1, . . . 9 to the commercial tail-weight categories >50, . . . <15.

ANNUAL LANDINGS AND CATCHES

During the second half of 1972, total landings by U.S.-flag vessels were 5.0 million pounds; in 1973 and 1974, they were 13.6 and 9.0 million pounds, respectively (Table 1). Landings of U.S. vessels were 50% and 39% of total international landings in 1973 and 1974. Monthly catches (Table 2) vary slightly from landings since they are estimated values and because catches are often landed in months subsequent to the month of capture.

To gain a perspective of the entire fishery, we assembled the historical landings of U.S.- and foreign-flag vessels for 1960–74 (Table 3, Figure 3) and the number of shrimp trawlers by country for 1961–74 (Table 4). There was a continuous increase in landings from 1960 (3.9 million pounds) through 1968 (27.3 million pounds). The landings declined slightly in 1969 and 1970 to 27.1 and 27.0 million pounds, respectively. There was a sharp decline in landings in 1971 and1972 (to 22 million pounds). In 1973 the fishery attained a maximum catch of 27.3 million pounds. The following year there was a decline in landings to 23.1 million pounds.

Ninety percent of the landings from 1960 through 1974 were made in Guyana (46%), French Guiana (21%), Surinam (14%), and Trinidad (10%). The remaining landings were made in Barbados (6%), Brazil (3%), and Venezuela (1%). National- and foreign-flag vessels landed in Barbados, Trinidad, Guyana, Surinam, and French

TABLE 1.—Landings of shrimp in pounds, heads-off weight, reported for U.S. vessels in the Guianas–Brazil shrimp fishery, 1972–74. This table is based on data submitted by processing plants; monthly data for January–June 1972 were not available.

Month of landing	1972	1973	1974
January		774,056	757,189
February		967,677	772,844
March		1,145,173	704,377
April		1,589,147	1,072,920
May		1,346,502	948,434
June		1,226,817	832,016
July	715,929	1,291,120	864,596
August	940,223	1,362,976	813,548
September	777,443	1,049,902	548,299
October	888,829	1,147,035	617,972
November	747,252	824,470	523,404
December	889,776	844,284	520,493
Total	4,959,452	13,569,159	8,976,092

TABLE 2.—Estimated total catch of shrimp in pounds, heads-off weight, by area of capture for U.S. vessels in the Guianas–Brazil shrimp fishery, 1972–74. Monthly data for January–June 1972 were not available.

Month of capture	1972			1973			1974		
	Zones 69–77	Zones 78–81	Total	Zones 69–77	Zones 78–81	Total	Zones 69–77	Zones 78–81	Total
January				884,040	—	884,040	924,749	—	924,749
February				943,550	—	943,550	558,397	—	558,397
March				354,064	1,028,331	1,382,395	405,853	635,532	1,041,385
April				319,021	1,214,699	1,533,720	434,842	597,420	1,032,262
May				349,367	838,737	1,188,104	415,514	497,284	912,798
June				480,020	805,609	1,285,629	352,805	448,404	801,209
July	253,057	561,134	814,191	541,619	969,059	1,510,678	337,820	566,662	904,482
August	560,547	316,461	877,008	464,255	690,750	1,155,005	240,074	502,583	742,657
September	425,187	410,184	835,371	386,446	737,912	1,124,358	269,655	266,952	536,607
October	550,666	337,679	888,345	531,989	482,733	1,014,722	428,949	114,212	543,161
November	649,768	149,558	799,326	518,332	238,878	757,210	512,751	11,956	524,707
December	713,867	—	713,867	669,802	—	669,802	318,141	—	318,141
Total	3,153,092	1,775,016	4,928,108	6,442,505	7,006,708	13,449,213	5,199,550	3,641,005	8,840,555

TABLE 3.—Annual landings of shrimp for the Guianas–Brazil shrimp fishery, 1960–74. Figures are in thousands of pounds, heads-off weight. Figures in parentheses are estimated values. Data for 1960–69 are from Naidu and Boerema (1972).

Year	Barbados	Trinidad	Venezuela	Guyana	Surinam	French Guiana	Brazil	Total
1960	—	—	—	3,568	381	—	—	3,949
1961	—	—	—	3,942	447	—	—	4,389
1962	—	—	—	5,126	1,072	—	—	6,198
1963	319	—	—	6,040	1,387	2,789	—	10,535
1964	1,481	—	—	6,984	1,709	2,961	—	13,135
1965	1,891	—	—	8,048	2,223	3,960	—	16,122
1966	2,400	2,386	—	9,546	2,943	4,668	—	21,943
1967	2,179	3,392	—	9,036	2,536	7,279	—	24,422
1968	2,570	4,280	—	9,161	3,438	7,860	—	27,309
1969	2,069	4,469	—	10,469	3,477	6,577	74	27,135
1970	1,339	4,373	—	11,807	3,534	4,867	1,137	27,057
1971	0	3,346	—	9,642	3,083	4,559	1,349	21,979
1972	0	2,082	—	10,743	3,518	4,553	(1,500)	22,396
1973	462	1,514	[1]2,454	12,000	3,949	5,442	(1,500)	27,321
1974	864	1,808	[2]NA	11,213	4,457	3,260	(1,500)	[3]23,102

[1]Novoa, D. 1974. Pesquería Venezolana en el área de las Guayanas durante 1973. Unpubl. manuscr., 14 p. FAO Governmental Consultation on Shrimp Resources in the CICAR Area, FIR: SR/74/NR-9.
[2]Not available.
[3]Does not include catch of 11 Cuban-flag trawlers.

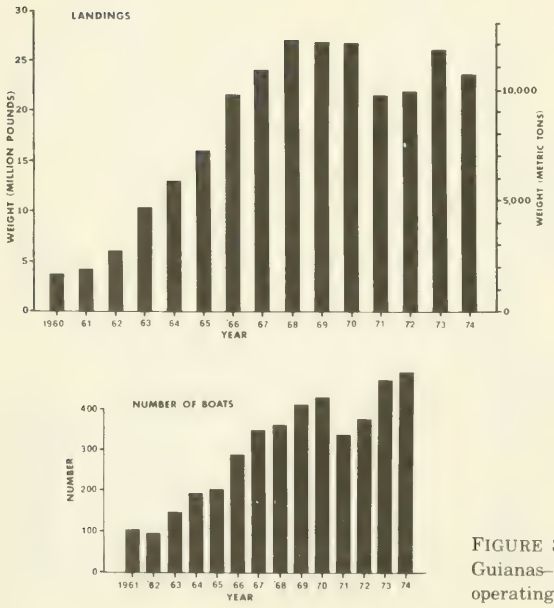

FIGURE 3.—Total landings of shrimp (heads off) for the Guianas–Brazil fishery, 1960–74 and the number of vessels operating each year. Data are from Tables 2 and 3.

Guiana; but only national-flag vessels operated in Brazil and Venezuela. The variation in landings between countries reflects mainly the differences in the sizes of the fleets supplying the processing plants in these countries (Table 3).

SPECIES COMPOSITION AND DISTRIBUTION

Our discussion about the species caught and their geographic distribution is based on data from logbooks. Vessel captains recorded a single, most abundant species to represent their daily catch; however, if two or more species were present, they recorded their catch as mixed. Single species were recorded in 58% of the catch and mixed species in 42%. Since the four species of shrimps are easily

TABLE 4.—Number of shrimp trawlers for the Guianas–Brazil shrimp fishery, 1961–74. The figures represent the average number of vessels fishing each year. Data for 1961–69 are from Naidu and Boerema (1972).

Year	Barbados	Trinidad	Venezuela	Guyana	Surinam	French Guiana (St. Laurent & Cayenne)	Brazil	Total
1961	—	—	—	60	40	—	—	100
1962	—	—	—	72	24	—	—	96
1963	—	—	—	89	25	33	—	147
1964	30	—	—	81	25	51 (20 + 31)	—	187
1965	24	—	—	96	25	58 (30 + 28)	—	203
1966	32	43	—	105	34	67 (28 + 39)	—	281
1967	32	58	—	113	50	89 (40 + 49)	—	342
1968	35	48	—	134	55	90 (53 + 37)	—	362
1969	36	63	—	142	51	110 (65 + 45)	1	403
1970	25	78	—	162	55	83 (37 + 46)	18	421
1971	—	60	—	160	45	60 (18 + 42)	21	346
1972	—	55	—	175	55	60 (17 + 43)	25	370
1973	6	42	[1]40	200	63	68 (22 + 46)	24	443
1974	21	39	[2]NA	202	106	62 (16 + 46)	30	[3]460

[1]In 1973, 80 Venezuela-flag trawlers operated for a 6-mo period.
[2]Not available.
[3]Does not include 11 Cuban-flag trawlers that fished with a mothership from March to December 1974.

distinguishable and there was no obvious bias in reporting species, we considered the single species to be representative of the entire daily catch, even though this overestimates the more abundant species. The composition of the catch for the entire area, according to this method, consisted of brown shrimp (70%), pink-spotted shrimp (23%), and other shrimps (7%) (Figure 4).

The geographic distribution of the different species of shrimps in the fishery is a subject of continuing research, but certain patterns in areal distribution were apparent (Figure 4). The areas off Guyana, Surinam, and western French Guiana (zones 69–75) were dominated by pink-spotted shrimp. Brown shrimp were listed more frequently off eastern French Guiana and Brazil (zones 76–81); white shrimp off Guyana (zones 69–71) and French Guiana and Brazil (zones 77–80); and pink shrimp off Guyana (zones 70–71).

We also examined the geographic distribution of the U.S.-vessel catch of all species. In 1972, U.S. vessels caught 36% of their catch in the Agreement Area off Brazil and 64% off the Guianas. The analogous catches for U.S. vessels in the Agreement Area were 52% (1973) and 41% (1974) (Table 2). Fishing off the Guianas (zones 69–77) was year-round. In the Agreement Area fishing by U.S. vessels was allowed 1 March–30 November (zones 78–80) and 1 March–30 June (zone 81).

Species composition of shrimp catches as reported by Japanese vessels[3] is in general agreement with our observations. Japanese catches off

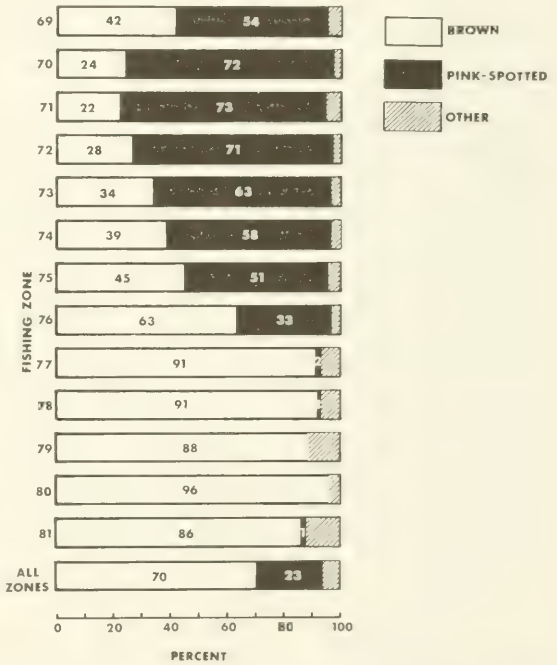

FIGURE 4.—Species composition by fishing zone of the shrimp catches of U.S. vessels in the Guianas–Brazil fishery for the period July 1972–December 1974. The data for this figure were calculated as explained in the text from the fishermen's logbooks.

Guyana and Surinam had higher percentages of "pink shrimp" (presumably mostly *P. brasiliensis*) than off French Guiana and Brazil. There were differences, however, between our data and the Japanese reports. Overall, brown shrimp were less prevalent in the Japanese catches than in the U.S. catches. The Japanese catch from 1969 to 1973

[3]Far Seas Fisheries Research Laboratory. 1971, 1972, 1973, 1974. South America north coast shrimp trawl fishing ground charts, 1969, 1970, 1971, 1972, 1973. Unpubl. manuscr., Far Seas Fish. Res. Lab., Shimizu.

was reported as 20%–35% brown shrimp (presumably *P. subtilis*) and 65%–80% pink shrimp (presumably mostly *P. brasiliensis*) (Far Seas Fisheries Research Laboratory see footnote 3).

SIZE COMPOSITION

The data on temporal and spatial distribution of sizes of shrimp provide information necessary for management of fishery stocks (Rounsefell and Everhart 1953). In particular, data on size reveal information on progressive changes as an indicator of rates of growth, population structure, maturity stages, and potential use of habitat by shrimp of different sizes, the latter being related to spawning, recruitment, and migration.

In our study the more precise data came from landing records, which we used to measure temporal changes in size composition. Size data from logbooks (less precise) were used to measure areal differences in size composition.

The majority of shrimp in U.S. landings for the entire period of 1972–74 were in the 26–30, 21–25, 16–20, and 11–15 tails-per-pound size categories (Figure 5). The sizes of shrimp caught may represent a true picture of size availability, but in many instances are also governed by factors which cause fishermen to select certain sizes (e.g., market price of shrimp, fuel price, feasibility of operation, and physical condition of the boat).

In studying the temporal and, to a lesser extent, the areal distribution of shrimp, we plotted from landing data the average size of shrimp for all ports combined and for Cayenne, French Guiana, only (Figure 6). The landings for all ports include catches from the entire fishery, while Cayenne landings reflect catches primarily off French Guiana and northern Brazil. The shrimp landed at Cayenne generally averaged slightly smaller than the shrimp from all ports combined. The smallest average size of shrimp, for both total landings and Cayenne landings, were in April and October in 1972 and 1973. In 1974, when fishing success was markedly lower than in 1973, small shrimp were present in October, but the expected April peak of small shrimp was less evident. Shrimp were larger in December–January and in June–August of each year.

Trends in average size of shrimp calculated from the logbook data were similar to those of average size calculated from the landing data (Figure 7). This similarity suggested that the size data from logbooks, although less precise, could also be used to compare areas; the smallest shrimp occurred in zones 69–70 and 77–81, and the largest in zones 71–76 (Figure 7). The magnitude of fluctuations in average size calculated from the log data were less than one size category unit, because the original data reported by fishermen are averages.

At present we have no satisfactory explanation for the greater prevalence of smaller shrimp off French Guiana and Brazil than in other areas of this fishery. We can offer some plausible hypotheses. Cayenne landings consist primarily of small brown shrimp caught off French Guiana and northern Brazil. These shrimp are probably recently recruited to the fishable population. Small

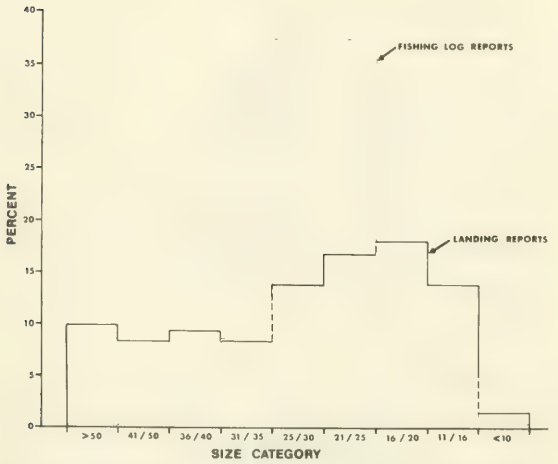

FIGURE 5.—Size composition of the shrimp catches of U.S. vessels as reported in landing records and fishing log reports for the period July 1972 to December 1974. The size categories given are the number of heads-off shrimp per pound.

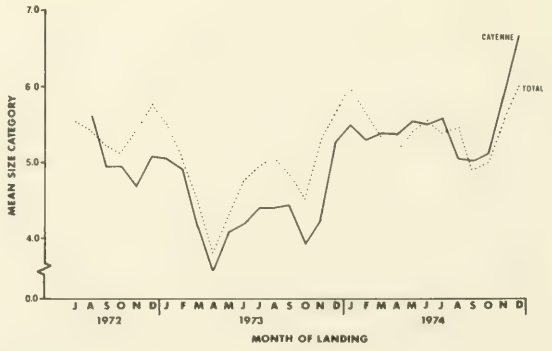

FIGURE 6.—Distribution by month of the mean size index of shrimp calculated from landing records of U.S. vessels at all ports of the Guianas shrimp fishery (marked as total on the graph) and at the Port of Cayenne, French Guiana. The size index was calculated as described in the text.

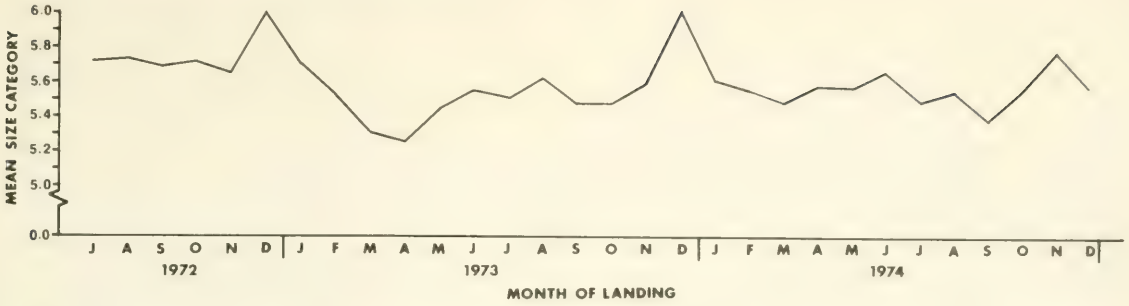

FIGURE 7.—Distribution by month and fishing zone of the mean size index of shrimp calculated from fishing log reports of U.S. vessels. The size index was calculated as described in the text.

shrimp also are present off Guyana. The smaller size of shrimp and higher catch rates in both areas, as compared with the larger shrimp and lower catch rates off Surinam, suggest that the East and West Grounds represent the principal areas of recruitment (Figure 1). Furthermore, the peaks of small shrimp in March, April, and October may indicate seasonal recruitment. Seasonal peaks in spawning and recruitment are common in penaeid shrimp populations, even where these activities occur throughout the year (Cook and Lindner 1970; Costello and Allen 1970). To determine the exact areas and chronology of recruitment for each species off the Guianas and northern Brazil will require additional research.

VARIATION IN CATCH RATES

Fishing success, or catch rate, provides a measure of the relative densities and availability of shrimp to the fishing gear and to the skilled fishermen. We examined the variations in catch rate by year, month, area, depth, and time of day to learn about the biology and ecology of the shrimp.

The average annual catch rates for U.S. vessels were 20.0 lb/fishing hour (1972 half year), 26.0 lb (1973), and 18.3 lb (1974). To observe the monthly differences in average catch rates off the Guianas and off Brazil we plotted catch rates for each statistical zone (Figures 8 and 9). Fluctuations in monthly catch rates followed a fairly regular pattern, peaking each year in March and April and then gradually declining during the remainder of the year. There were smaller peaks in July and August (Figure 8). Catch rates were consistently higher off Brazil (zones 78–81) than off the Guianas (zones 69–77). The highest catch rates were recorded in zones 78–81, intermediate in zones 75–77 and 69–71, and lowest in zones 72–74 (Figure 9).

Information on water depth without specific knowledge of the type of sediment, chemical content of water masses, and information on water temperature and speed and direction of the current means little in ecological terms. But, in a pragmatic sense, the statistics on shrimp catches versus depth are important. In our study the distribution of shrimp catches varied with water

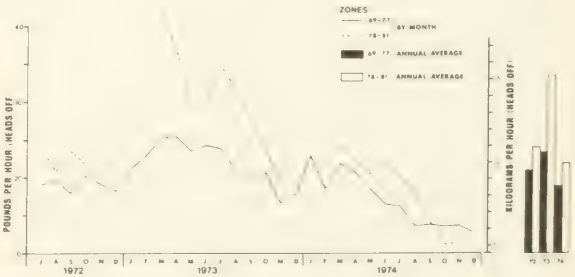

FIGURE 8.—Distribution by month of the mean catch rate of shrimp for U.S. vessels fishing off the Guianas (zones 69–77) and off Brazil (zones 78–81), July 1972 to December 1974. Catch rate is expressed as pounds and kilograms of shrimp (heads-off weight) per hour of fishing.

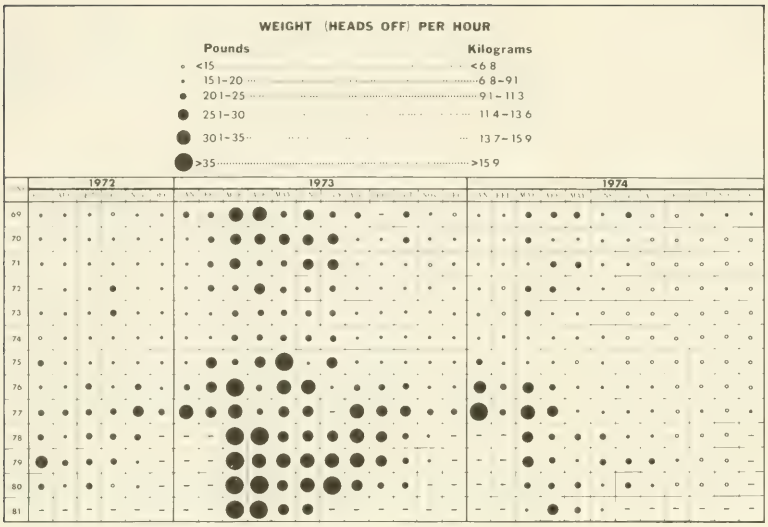

FIGURE 9.—Distribution by month and fishing zone of the mean catch rate of shrimp for U.S. vessels fishing in the Guianas–Brazil fishery, July 1972 to December 1974. See Figure 1 for location of fishing zones. Catch rate is expressed as pounds (and kilograms) of shrimp (heads-off weight) per hour of fishing.

depth. The average catch rates were: 35.4 lb/h (0–5 fm), 25.0 lb/h (6–10 fm), 21.5 lb/h (11–15 fm), 20.5 lb/h (16–20 fm), 21.1 lb/h (21–25 fm), 20.7 lb/h (26–30 fm), 21.1 lb/h (31–35 fm), 23.2 lb/h (36–40 fm), 22.7 lb/h (41–45 fm), and 24.5 lb/h (46–60 fm). Off Guyana, Surinam, and French Guiana (zones 69–77), average catches were lower at the intermediate depths (16–35 fm) than in shallower or deeper water (Figure 10). Off Brazil the average catch did not vary with depth in zones 78 and 79, but in zones 80 and 81 average catches were higher at the intermediate depths than in shallower or deeper water.

We also examined the distribution of fishing effort in relation to depth. Fishing effort was concentrated primarily in intermediate depths. Sixty percent of the fishing effort reported in logbooks occurred between 21 and 35 fm, 18% in <20 fm, and 22% in >36 fm. Off Guyana, Surinam, and French Guiana most fishing was between 16 and 30 fm; off Brazil, it was in deeper water (Figure 11). While the highest catch rates were usually in the shallow and deep zones at the edge of the fishing grounds, these areas supported only a small percentage of the total fishing effort. Shallow and deep zones probably were fished only when good catches could be made, whereas the intermediate depths were fished during times of both good and poor fishing.

The availability of shrimp to the fishermen in relation to time of day varies for each area, species, and time of the year. Most fishing for shrimp was done at night, some during the day, and some on a 24-h/day basis (Figures 12 and 13). The time spent fishing at night was three times that spent during the day. White shrimp were caught primarily during daylight hours off the Guianas and fishing in the East Gullies (zone 79) was usually done during the day. In the Drop-Off and Steeples (zones 80–81), fishing on a 24-h/day basis made up nearly half the total fishing time. The average catch rates for the entire fishery were 29.6 lb/h (day fishing), 18.9 lb/h (night fishing), and 22.1 lb/h (day and night fishing). The mean catch rates were higher for day fishing than night in all zones and at all depth intervals. We conclude that the usual strategy is to fish at night, except for certain species (e.g., white shrimp) or in certain areas (e.g., East Gullies) where day fishing is more successful. During periods of high catches, fishing is usually carried out on a 24-h/day basis until a full catch is made or until the fishermen are exhausted.

APPRAISAL OF THE FISHERY

The fishery for shrimp in the Guianas–Brazil area reached a historical maximum annual production of 27.3 million pounds heads-off in 1973. We used a surplus yield model to estimate the maximum sustainable yield of the resource (Fox 1970). We also compared predicted annual equilibrium yields with actual annual yields attained to measure the expected variation from equilibrium conditions.

An exponential surplus yield model suggested

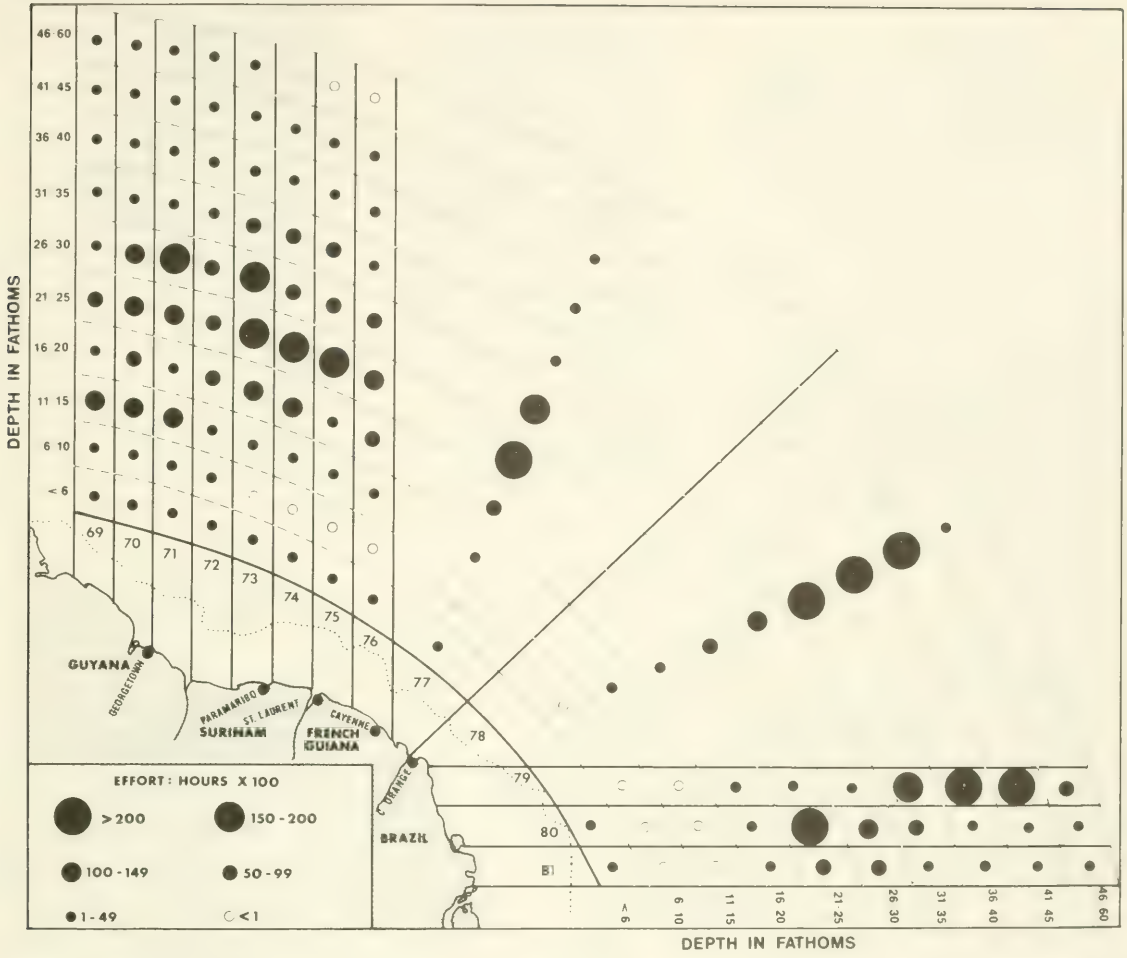

FIGURE 10.—Distribution by fishing zone and water depth of the fishing effort reported on logbooks by U.S. vessels in the Guianas-Brazil fishery, July 1972 to December 1974.

that the maximum sustainable yield was 28.7 million pounds, which could be taken by 692 vessels. This estimate was made from the relationship between the logarithm of the annual catch per vessel and average number of vessels (r = 0.80) for the years 1965–74. A linear surplus yield model applied to the data for the same years suggested that the maximum yield was 27.1 million pounds, which could be taken by 531 vessels (r = 0.82) (Figure 14).

The average number of vessels is the only index of total effort available for the fishery before 1972. The double-rigged Florida-type shrimp trawler has been, almost without exception, the only type vessel used in the fishery. Increases in fishing efficiency probably occurred as the length and horsepower of the vessels increased (Jones and Dragovich 1973), and as the addition of refrigeration equipment permitted longer and farther ranging fishing trips; but these changes were minor in the 1965–74 period.

Before 1965 the increase in average annual catch per vessel paralleled the increase in fleet size (Table 5). The catch per vessel rose sharply between 1961 and 1962; from 1962 to 1965 the increase continued but was less pronounced. Presumably, during these early years of the fishery, the efficiency of the fleet increased as familiarity was gained with the fishing grounds. The earlier data, therefore, were not used in the model. After

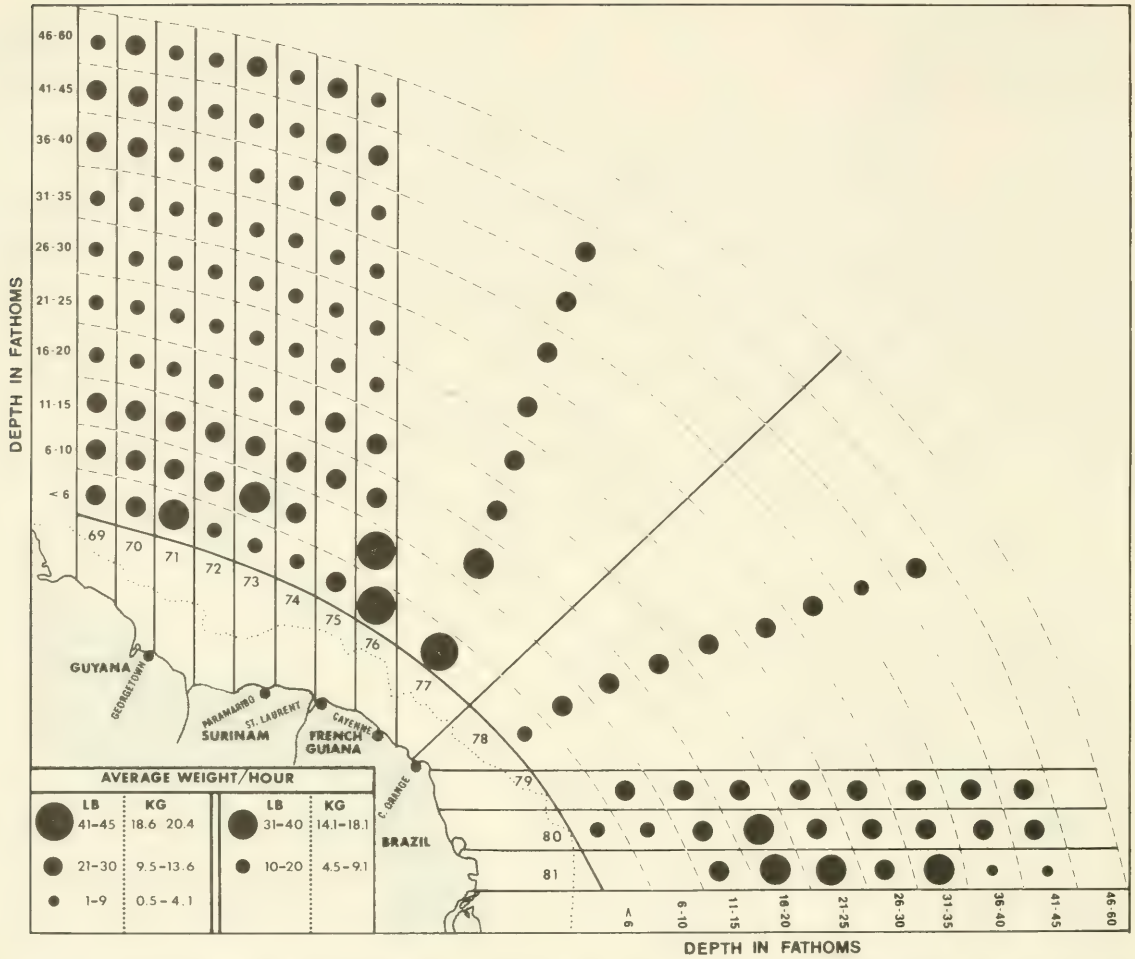

FIGURE 11.—Distribution by fishing zone and depth of the mean catch rate of shrimp for U.S. vessels fishing in the Guianas–Brazil fishery, July 1972 to December 1974. Catch rate is expressed as pounds (and kilograms) of shrimp (heads-off weight) per hour of fishing.

1964, the decline in the average production per vessel was consistent with the increase in the number of vessels. The average annual production per vessel declined from 79,000 lb of shrimp in 1965 to 50,000 lb in 1974; during this time the fleet size increased from 203 vessels (1965) to 460 vessels (1974).

The decline in annual catch per vessel suggests that the average abundance of shrimp available to the fishery has decreased as a result of fishing. Total yields, however, are not depressed at present levels of fishing effort. Apparently the productivity of the resource allows the present level of commercial harvest and also sufficient recruitment to the next generation.

Surplus yield models have been applied in shrimp fishery analysis, though certain assumptions in their use are not completely valid, e.g., instantaneous recruitment, equilibrium conditions, and behavior of the species and populations as a single unit. Also, there is no evidence that the abundance of shrimp recruits is dependent on the abundance of the parent stock in this fishery. Therefore, the prediction of maximum equilibrium yield by a surplus yield model, should be interpreted with caution, especially when the maximum is predicted to occur at fishing effort levels beyond those observed.

The historical shrimp catches follow closely the trends predicted by the surplus yield model (Fig-

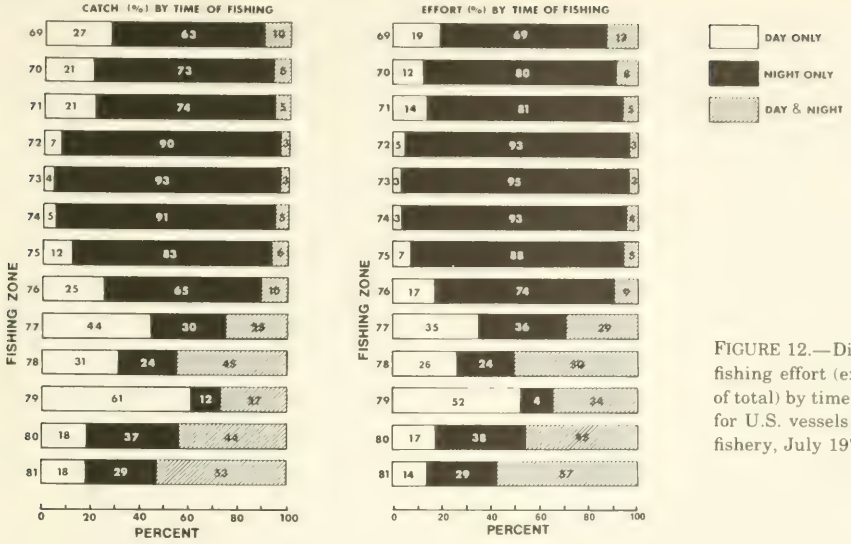

FIGURE 12.—Distribution of catch and fishing effort (expressed as percentage of total) by time of day and fishing zone for U.S. vessels in the Guianas–Brazil fishery, July 1972 to December 1974.

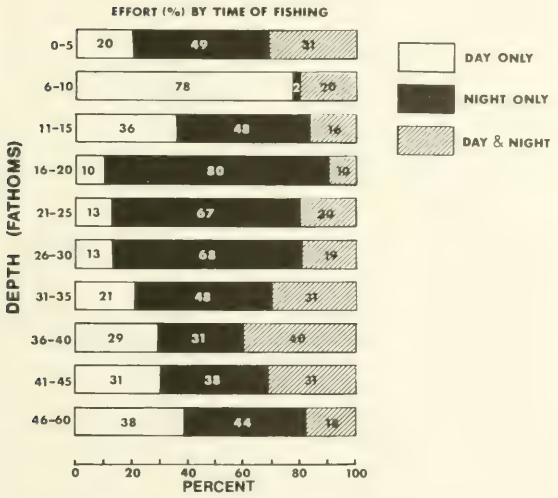

FIGURE 13.—Distribution of fishing effort (expressed as percentage of total) by time of day and water depth for U.S. vessels in the Guianas–Brazil fishery, July 1972 to December 1974.

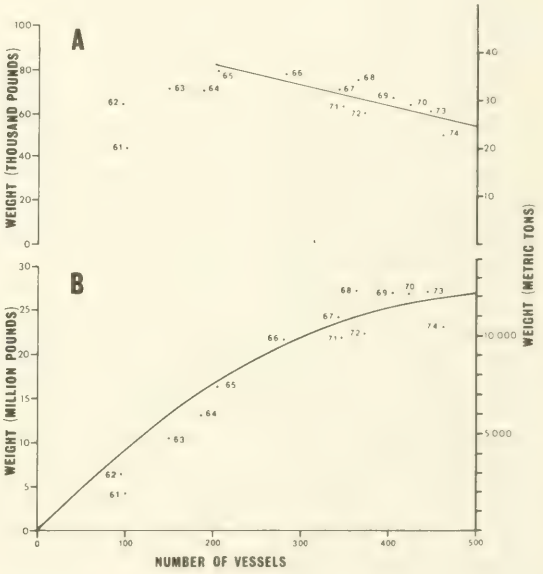

FIGURE 14.—Relationship of the average annual landings per vessel (A) and the total production of shrimp (B) to the total estimated fishing effort (average number of vessels operating) for the Guianas–Brazil shrimp fishery. The linear trend line shown was fitted to the data for the years 1965–74; the estimated production curve was derived from the line in A. The exponential trend line was calculated as explained in the text but is not shown in this figure.

ure 14). From 1961 to 1968 the total production from the fishery rose in proportion to the increase in the number of fishing vessels. In 1969 and 1970 fishing effort increased, but production remained constant at 27 million pounds. Fishing was reduced in 1971 and the catch, therefore, declined. After 1971, catch and effort continued upwards at rates similar to those in the early years of the fishery and a catch of 27 million pounds was again attained in 1973. In 1974 the number of vessels remained high, but the catch declined to 23 million pounds.

The variation of the annual catches from those predicted by the model were 53% and 31% in 1961

TABLE 5.—Average annual catch of shrimp (in pounds, heads-off weight) per vessel by country. Data are derived from Tables 3 and 4.

Year	Barbados	Trinidad	Venezuela	Guyana	Surinam	French Guiana	Brazil	Total
1961	—	—	—	65,700	11,175	—	—	43,890
1962	—	—	—	71,194	44,667	—	—	64,562
1963	—	—	—	67,865	55,480	84,515	—	71,667
1964	49,367	—	—	86,222	68,360	58,059	—	70,241
1965	78,792	—	—	83,833	88,920	68,276	—	79,419
1966	75,000	55,488	—	90,914	86,559	69,672	—	78,089
1967	68,094	58,483	—	79,965	50,720	81,787	—	71,409
1968	73,429	89,167	—	68,366	62,509	87,333	—	75,439
1969	57,472	70,937	—	73,725	68,176	59,791	74,000	67,333
1970	53,560	56,064	—	72,883	64,255	58,639	63,167	64,268
1971	—	55,767	—	60,263	68,511	75,983	64,238	63,523
1972	—	37,855	—	61,389	63,964	75,883	60,000	60,530
1973	77,000	36,048	61,350	60,000	62,683	80,029	62,500	61,673
1974	41,143	46,359	—	55,510	42,047	52,581	50,000	50,222

and 1962, respectively, but for 1963–74 they ranged from 3% to 18%, averaging 8.5%. These variations in catches are deviations about the mean condition predicted by the model. The deviations include the effects of dynamic environmental conditions, but also include random variations and the failure of the model to predict the effects of fishing.

The *Penaeus* shrimp fishery operates mostly on a single year class and year-to-year fluctuations in shrimp populations are to be expected because of the short life cycle of the species. Fluctuations in the annual yield of shrimp are partly the result of variations in spawning success and in survival of young in the inshore nursery grounds, which are generally subject to more extreme variations in environmental conditions than the offshore habitat of adult shrimp. An important management problem for this shrimp fishery is to predict and utilize annual fluctuations in the populations, rather than to only predict an equilibrium yield at a constant level of fishing effort. This will require more detailed knowledge of growth, mortality, and recruitment patterns of the shrimp and the application of yield-per-recruit and stock-recruitment models.

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APPENDIX TABLE 1.—Catches by area and month for the Guianas–Brazil shrimp fishery reported by U.S. vessels. Catches are reported by month in which capture was made; landings are reported by month in which trip was completed.

Item	1972 July	Aug.	Sept.	Oct	Nov.	Dec.
Catches:						
Zones 69–77:						
No. drags	501	2,433	2,301	2,740	3,269	3,473
No. hours	2,950	12,705	12,815	14,809	18,580	19,666
Catch (pounds[1])	56,530	250,097	230,857	300,346	357,385	361,234
Catch/drag	112.8	102.8	100.3	109.6	109.3	104.0
Catch/hour	19.2	19.7	18.0	20.3	19.2	18.4
Zones 78–81:						
No. drags	909	1,184	1,643	1,537	737	
No. hours	5,234	6,785	9,485	8,477	4,120	
Catch (pounds[1])	125,351	141,194	222,711	184,178	82,260	
Catch/drag	137.9	119.3	135.6	119.8	111 6	
Catch/hour	23.9	20.8	23.5	21.7	20.0	
Total:						
No. drags	1,414	3,617	3,946	4,285	4,006	
No. hours	8,205	19,490	22,310	23,334	22,700	
Catch (pounds[1])	182,311	391,291	454,518	485,894	439,645	
Catch/drag	128.9	108.2	115.2	113.4	109.7	
Catch/hour	22.2	20.1	20.4	20.8	19.4	
Landings (pounds[1])	715,929	940,223	777,443	888,829	747,252	889,776
Percent of landings reported on fishing logs	6.1	34.8	56.5	52.6	57.2	53.1

Item	1973 Jan.	Feb.	Mar.	Apr.	May	June
Catches:						
Zones 69–77:						
No. drags	3,636	3,119	1,308	1,289	1,580	2,216
No. hours	20,522	16,996	6,804	7,154	8,692	12,677
Catch (pounds[1])	437,420	390,142	172,585	181,845	205,385	309,276
Catch/drag	120.3	125.1	131.9	141.1	130.0	139.6
Catch/hour	21.3	23.0	25.4	25.4	23.6	24.4
Zones 78–81:						
No. drags			2,366	3,511	3,024	3,208
No. hours			12,005	18,694	16,888	17,435
Catch (pounds[1])			501,250	692,390	493,075	519,053
Catch/drag			211.8	197.2	163.0	161.8
Catch/hour			41.8	37.0	29.2	29.8
Total:						
No. drags			3,682	4,883	4,629	5,461
No. hours			18,857	26,022	25,726	30,334
Catch (pounds[1])			674,735	882,175	700,950	832,369
Catch/drag			183.2	180.7	151.4	152.4
Catch/hour			35.8	33.9	27.2	27.4
Landings (pounds[1])	774,056	967,677	1,145,173	1,589,147	1,346,502	1,226,817
Percent of landings reported on fishing logs	47.9	53.2	35.2	58.6	56.2	62.1

Item	1973 July	Aug.	Sept.	Oct.	Nov.	Dec.
Catches:						
Zones 69–77:						
No. drags	2,450	2,007	1,675	2,144	2,422	3,249
No. hours	13,772	11,932	9,663	12,023	14,254	18,683
Catch (pounds[1])	329,048	251,585	192,636	249,005	237,945	332,835
Catch/drag	134.3	121.1	115.0	116.1	98.2	102.4
Catch/hour	23.9	21.1	19.9	20.7	16.7	17.8
Zones 78–81:						
No. drags	2,922	2,118	2,362	2,746	948	
No. hours	16,920	11,814	13,323	9,612	5,683	
Catch (pounds[1])	588,729	374,325	367,835	225,950	109,200	
Catch/drag	201.5	176.7	155.7	129.4	115.2	
Catch/hour	34.8	31.7	27.6	23.5	19.2	
Total:						
No. drags	5,409	4,195	4,037	3,903	3,370	
No. hours	30,914	23,746	22,986	21,723	19,937	
Catch (pounds[1])	922,557	625,910	560,471	476,785	347,145	
Catch/drag	170.6	149.2	138 8	122.2	103.0	
Catch/hour	29.8	26.4	24.4	21.9	17.4	
Landings (pounds[1])	1,291,120	1,362,976	1,049,902	1,147,035	824,470	844,284
Percent of landings reported on fishing logs	67.3	55.2	52.9	47.0	46.9	44.9

[1]Heads-off weight.

APPENDIX TABLE 1.—Continued.

Item	1974 Jan.	Feb.	Mar.	Apr.	May	June
Catches:						
Zones 69–77:						
No. drags	4,028	3,425	2,348	2,473	3,103	2,563
No. hours	22,242	19,319	12,167	12,471	15,962	14,816
Catch (pounds[1])	509,163	360,836	266,896	259,317	297,838	246,021
Catch/drag	126.4	105.3	113.7	104.9	96.0	96.0
Catch/hour	22.9	18.7	21.9	20.8	18.6	16.6
Zones 78–81:						
No. drags			3,145	2,845	3,039	2,531
No. hours			17,152	16,011	17,388	13,878
Catch (pounds[1])			417,937	356,270	356,450	312,685
Catch/drag			132.9	125.2	117.3	123.5
Catch/ hour			24.4	22.2	20.5	22.5
Total:						
No. drags			5,551	5,354	6,190	5,163
No. hours			29,649	28,712	33,696	29,203
Catch (pounds[1])			691,463	624,907	664,083	571,941
Catch/drag			124.6	116.7	107.3	110.8
Catch/hour			23.3	21.8	19.7	19.6
Landings (pounds[1])	757,189	772,844	704,377	1,072,920	94,834	832,016
Percent of landings reported on fishing logs	55.1	59.2	79.3	58.0	63.5	83.3

Item	1974 July	Aug.	Sept.	Oct.	Nov.	Dec.
Catches:						
Zones 69–77:						
No. drags	2,183	1,977	2,131	2,813	3,478	3,038
No. hours	13,059	11,599	12,156	16,936	20,658	18,482
Catch (pounds[1])	213,244	159,665	167,545	229,588	282,405	237,991
Catch/drag	97.7	80.8	78.6	81.6	81.2	78.3
Catch/hour	16.3	13.8	13.8	13.6	13.7	12.9
Zones 78–81:						
No. drags	2,975	3,063	1,959	873	91	
No. hours	17,640	18,486	11,724	5,427	577	
Catch (pounds[1])	375,697	334,250	165,865	61,130	6,585	
Catch/drag	120.2	109.1	84.7	70.0	72.4	
Catch/hour	20.3	18.1	14.1	11.3	11.4	
Total:						
No. drags	5,158	5,040	4,090	3,686	3,569	
No. hours	30,699	30,085	23,880	22,363	21,235	
Catch (pounds[1])	571,961	494,915	333,410	290,718	288,990	
Catch/drag	110.9	98.2	81.5	78.9	81.0	
Catch/hour	18.6	16.4	14.0	13.0	13.6	
Landings (pounds[1])	864,569	813,548	548,299	617,972	523,404	520,493
Percent of landings reported on fishing logs	59.9	66.8	66.4	58.4	47.8	62.4

[1]Heads-off weight.

SEASONAL CYCLE OF ZOOPLANKTON ABUNDANCE AND SPECIES COMPOSITION ALONG THE CENTRAL OREGON COAST

WILLIAM T. PETERSON AND CHARLES B. MILLER[1]

ABSTRACT

Species composition of zooplankton collected during 3 yr of sampling close to the coast at Newport, Oreg., varied with season. In all seasons the most abundant plankters were copepods. Dominant species in summer were *Pseudocalanus* sp., *Acartia clausii, A. longiremis, Calanus marshallae,* and *Oithona similis.* These are primarily coastal forms with northern affinities, and they were present all year. Dominant species in winter were *Paracalanus parvus* and *Ctenocalanus vanus,* forms of southern affinities. They tended to disappear completely in summer. These geographic affinities are in correspondence with the source regions for surface waters that are implied by the direction of flow in the different seasons. Abundances are about one order of magnitude higher in summer than in winter. Copepod diversity is greater in winter than summer: the winter checklist contains 51 species, while the summer list contains only 38 species.

An analysis of differences in the zooplankton of the three winter periods of the study shows 1969–70 to have had much greater dominance by southern forms and a larger variety of them than 1970–71 or 1971–72. This corresponds with differences in the wind patterns between the years. Winds in the winter of 1969–70 were gentle and directly from the south, while the other winters had the more usual southwesterly storms. Gentle winds directly from the south were more effective at moving surface water northward alongshore than southwesterly storms, despite their lesser overall northerly component.

The hydrography and pelagic ecology of the Pacific Ocean very close to the Oregon coast are strongly seasonal. Winter winds from the southwest, which produce surface flow from the south and toward shore, alternate with summer winds from the north, which produce flow from the north and away from shore, generating coastal upwelling. These seasonal changes in the source of currents flowing through the area cause changes in the species of zooplankton that are present. In this paper we describe this cycle of change in species composition from a series of samples collected along a transect normal to the coast at Newport, Oreg., approximately every 2 wk from June 1969 through July 1972. In a previous paper (Peterson and Miller 1975) we have used these data to make a detailed comparison of the upwelling seasons of the years 1969, 1970, and 1971 with emphasis upon the differences between years. Here we consider the entire annual cycle with emphasis upon consistent aspects of the differences between seasons. The discussion includes a consideration of the differences between the three winters of the study.

MATERIALS AND METHODS

Detailed description of collection and laboratory procedures are given in Peterson and Miller (1975, 1976). Plankton samples were collected with a 240-μm mesh net hauled obliquely from near the bottom to the surface at stations 2, 5, 9, and 18 km from the Oregon coast along a transect at lat. 44°40′N. The stations will be referred to as NH 1, NH 3, NH 5, and NH 10, respectively, which stand for Newport Hydrographic stations at 1, 3, 5, and 10 n.mi. from the shore. Water depths for the four stations were 20, 46, 55, and 80 m. Surface temperature and salinity measurements were made at most stations, and a bathythermograph was usually lowered. A total of 213 samples from 56 dates are included in the present analyses. Distribution of samples among stations, exact dates, and complete data for all samples can be found in Peterson and Miller (1976).

There are important limitations on the zooplankton data. We chose to express numerical abundance as numbers of individuals per cubic meter (no. m^{-3}). Because our nets were towed obliquely through the entire water column, the quantitative abundance estimates are actually abundances averaged over the water column. If an

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animal is equally abundant at all depths, then oblique tows will adequately estimate its abundance. If an animal is restricted to a narrow surface layer, then its abundance will be underestimated by deeper tows relative to shallower ones. Recent work by ourselves and Myers (1975) has shown that highest zooplankton abundances are found within the top 20 to 30 m of the water column. Therefore, our oblique tows from depths greater than about 30 m do underestimate zooplankton abundances. This becomes a problem for tows taken at stations farther from shore as the water depth increases, because an increasing fraction of the water column sampled contains few animals. Therefore, abundance gradients should not be considered to be real between stations NH 1 (water depth = 20 m) and NH 10 (water depth = 80 m) unless abundance differences are greater than a factor of four.

Abundances are also underestimated for many copepod taxa because the small copepodite stages could easily pass through our 240-μm mesh net. Copepodites of species of *Pseudocalanus* and *Acartia* younger than stage III were seldom seen in our samples. Probably only stages IV and V were sampled quantitatively.

The data set gains its value from being a 3-yr time series of samples collected in exactly the same manner at the same stations. As such, these are good baseline data to which future work can be compared. Point estimates of abundance have little meaning, but comparisons of abundances between seasons and years at a set of stations are valid and meaningful.

TABLE 1.—A checklist of copepod species taken off Newport, Oreg., in summer (S) and winter (W) months during the period of the study.

[C = Common, occurrence in >50% of the samples taken, U = Unusual, occurrence in <50% but >5 samples taken, R = Rare occurrence <5 samples.]

Copepod species	S	W	Copepod species	S	W
Calanus marshallae	C	C	*Metridia lucens*[2]	C	C
C. tenuicornis	U	C	*M. pacifica*[2]	U	
C. plumchrus	R	U	*Lucicutia flavicornis*	U	U
C. cristatus		R	*Candacia columbiae*		R
Rhincalanus nasutus	R	R	*C. bipinnata*	R	R
Eucalanus bungii	U	U	Immature *Heterorhabdus*		
Mecynocera clausii		U	spp.		R
Paracalanus parvus	C	C	*Pleuromamma borealis*		R
Calocalanus styliremis		U	*P. abdominalis*		R
C. tenuis		U	*Centropages abdominalis*	C	U
C. sp		R	*Epilabidocera amphitrites*	U	U
Pseudocalanus sp.[1]	C	C	*Acartia clausii*	C	C
Microcalanus pusillus	U	U	*A. longiremis*	C	C
Clausocalanus masti-			*A. tonsa*	U	C
gophorus		U	*A. danae*		R
C. furcatus		R	*Eurytemora americana*	R	
C. arcuicornis	U	C	*Tortanus discaudatus*	U	U
C. jobei		R	*Microsetella* sp	U	U
C. pergens	U	C	*Sapphirina* sp.	U	U
C. parapergens		U	*Oithona similis*	C	C
C. paululus		R	*O. spinirostris*	C	C
Ctenocalanus vanus	U	C	*Oncaea tenella*	R	R
Aetideus pacificus	U		*O. borealis*	R	R
Immature *Gaidius* spp.	U		*O. conifera*	R	R
Gaidius brevispinus		R	*O. mediterranea*	R	R
Immature *Gaetanus* spp.	R		*O. dentipes*		R
Gaetanus simplex		R	*O. subtilis*		R
Paraeuchaeta japonica	R	R	*O. media hymena*	R	
Racovitzanus antarcticas	U		*Corycaeus anglicus*	R	C
Scolecithricella minor	U	U	*C. amazonicus*		R

[1]Pacific representatives of the genus *Pseudocalanus* are not adequately described. They are being studied by B. Frost.

[2]Two morphs of the genus *Metridia* were separated on the basis of the shape of the prosome in lateral view. The *M. pacifica* type is more robust and has a steeply sloping forehead. Detailed morphological analysis of the two types has not been done.

RESULTS

Frequency of Occurrence of Zooplankton Taxa

Copepods were the most frequently occurring and the most abundant members of the zooplankton community in the nearshore region off Newport, Oreg. Fifty-eight species were seen in our samples (Table 1). Thirty-eight species were found in the summer samples and 51 species in the winter samples. During our study, species from the Subarctic, Transition, and Central Pacific faunal groups (McGowan 1971) were taken.

The copepods in Table 1 can be grouped on the basis of patterns of occurrence. Eight species occur commonly during both winter and summer months: *Calanus marshallae, Paracalanus parvus, Psuedocalanus* sp., *Metridia lucens, Acartia clausii, A. longiremis, Oithona similis,* and *O. spinirostris.* Seven species were found only during the summer months and probably have northern affinities: *Aetideus pacificus, Gaidius* immatures, *Gaetanus* immatures, *Racovitzanus antarcticas* s.l., *Metridia pacifica,* and *Oncaea media hymena. Eurytemora americana* occurred very rarely in the sample series, but it is a common form in all of the local estuaries (Frolander et al. 1973). Only one species was common during the summer and uncommon during the winter: *Centropages abdominalis.* This species has northern affinities. A group of six species had the opposite characteristic; that is, they were common during the winter but uncommon or rare during the summer: *Calanus tenuicornis, Clausocalanus arcuicornis, C. pergens, Ctenocalanus vanus* s.l., *Acartia tonsa,* and *Corycaeus anglicus.* All of these species are common in warmer water south of Oregon.

The majority of the copepod species (43) were

always uncommon or rare in our samples and probably have unimportant roles in the community. However, taxonomic study of these rare or uncommon species is important because in many cases their presence indicates the presence of a particular water type or mixture of types. Most of the species that are found off Newport only during winter months have southern affinities (Central Pacific waters). They are transported north along the continental shelf by the Davidson Current and are probably very near the extreme northerly limit of their range. These species were *Mecynocera clausii, Calocalanus styliremis, C. tenuis, Calocalanus* sp., *Clausocalanus mastigophorus, C. furcatus, C. jobei, C. parapergens, C. paululus, Acartia danae, Corycaeus amazonicus, Oncaea dentipes,* and *O. subtilis*. Other species that were found only during winter months have northern affinities and are usually found in deep water over the continental slope. They were probably transported shoreward as a result of onshore winds. These species were *Calanus cristatus, Gaidius brevispinus, Gaetanus simplex, Candacia columbiae, Heterorhabdus* immatures, *Pleuromamma borealis,* and *P. abdominalis*. The 16 species that were rare or uncommon in both summer and winter include representatives of both northern and Central Pacific faunal groups.

Seasonal Cycle of Total Zooplankton Abundance

The annual cycles of total zooplankton abundance for stations NH 1, NH 3, NH 5, and NH 10 are shown in Figures 1, 2, and 3. Abundance is high during the upwelling season and often remains high during the autumn period of hydrographic transition. Abundance is low during the period from November through April. All four stations have this basic pattern, but there are important changes with distance offshore. Table 2 gives several indices of cycle amplitude. The amplitude of the cycle is greater inshore. First, there are more dates at NH 1 and NH 3 with densities in excess of 5,000 m^{-3} (an arbitrary value). Second, the absolute difference between summer and winter density decreases with distance from shore. All of the decrease in the ratio of the densities in the two seasons occurs between 2 and 5 km from shore (NH 1 to NH 3).

There is a suggestion in the data for NH 1 (Figure 1) that the annual cycle of zooplankton abundance is more complex than just a summer high

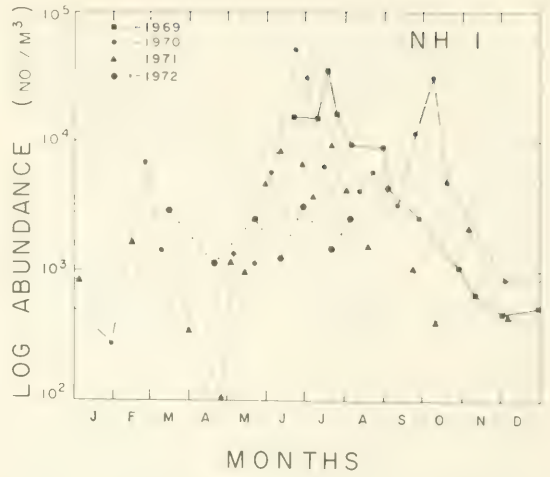

FIGURE 1.—Annual cycle of totaled zooplankton abundance 2 km from the Oregon coast at Newport (NH 1) during the 3-yr study period.

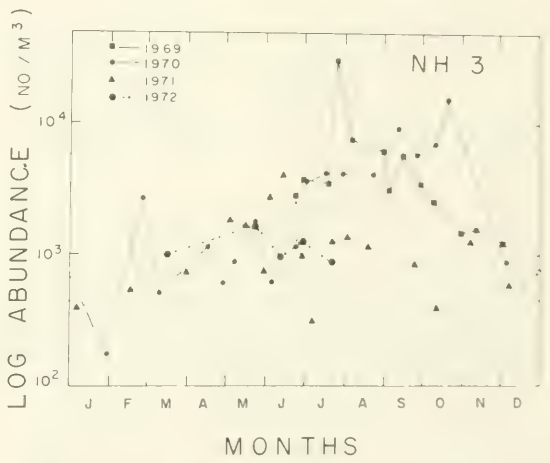

FIGURE 2.—Annual cycle of totaled zooplankton abundance 5 km from the Oregon coast at Newport (NH 3) during the 3-yr study period.

TABLE 2.—Some indices of the amplitude of the seasonal cycle of zooplankton density off the Oregon coast. Median density estimates for summer and winter seasons at the four stations on the Newport, Oreg., transect, the ratio of median densities between seasons, and the number of dates with densities >5,000 m^{-3}.

Station	Summer (May–Oct.)	Winter (Nov.–Apr.)	Summer–winter ratio	No. dates with density >5,000 m^{-3}
NH 1	4,350 m^{-3}	850 m^{-3}	5.1	17
NH 3	2,250 m^{-3}	800 m^{-3}	2.8	8
NH 5	1,550 m^{-3}	530 m^{-3}	2.9	4
NH 10	1,000 m^{-3}	365 m^{-3}	2.7	0

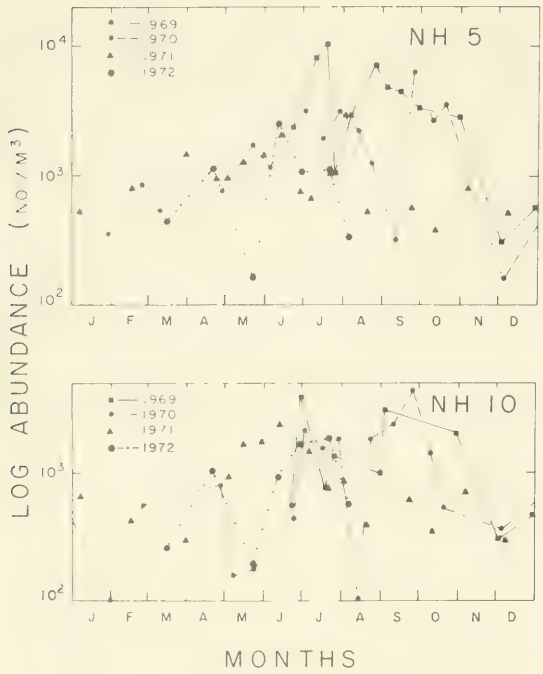

FIGURE 3.—Annual cycle of totaled zooplankton abundance 9 and 18 km from the Oregon coast at Newport (NH 5 and NH 10) during the 3-yr study period.

and a winter low. In addition to that basic cycle, there are peaks in total abundance at NH 1 in each year of the study in either February or March. The 25 February 1970 sample had high numbers of copepod nauplii other than *Calanus* (1,840 m^{-3} = 27% of the total zooplankton). This indicates the presence of an actively reproducing adult copepod population. A diatom bloom was in progress at that time as well. Our nets were clogged with the diatom *Thalassiosira*. The 16 February 1971 peak had high numbers of *Pseudocalanus* sp. (680 m^{-3} = 41% of the catch), *Calanus marshallae* (240 m^{-3} = 15%), and *Calanus* nauplii (192 m^{-3} = 12%). The *Pseudocalanus* sp. population was almost entirely stage I copepodites. These facts again indicate actively reproducing adult copepod populations in late winter. In both of these years, abundances decreased after the February peak to lower values in March or April. In 1972 no samples were collected in January or February. The 15 March sample at NH 1 had high numbers of *Pseudocalanus* sp. (1,844 m^{-3} = 62%), *Oithona similis* (690 m^{-3} = 23%), and *Acartia longiremis* (265 m^{-3} = 9%). Half of the total catch were immature *Pseudocalanus* sp. and half of the *A. longiremis* were immature. Again, there is some evidence of a late winter cycle of reproduction of the species of copepods permanently resident in the nearshore zone and dominant later in the year. There is evidence of this late winter peak in copepod abundance at NH 3 only in 1970, and it is not seen at all in the data for NH 5 and NH 10.

The months of April and May are periods of transition in the direction of the prevailing wind. An atmospheric high pressure cell begins to form over the North Pacific Ocean, and the winds begin to blow from the north with greater frequency. In all years of this study, heavy phytoplankton blooms were observed at NH 1 during this period. The blooms are probably associated with the replenishment of nutrients within the photic zone by the earliest brief episodes of upwelling. Dates with dense blooms were 27 April 1970, 3 and 14 May 1971, 20 April 1972, and 22 May 1972. Zooplankton abundances were low at these times.

Seasonal Cycle of Relative Species Abundance

The seasonal cycle of relative abundance of the most abundant species of copepods is shown in Figure 4 for all four stations. The graphs for each station represent cumulative percentage of the total catch for the species as labelled. The result is complex but deserves careful study because some interesting patterns are present. The simplest pattern is the sinusoidal annual cycle. This pattern is in phase with the seasonal cycle of total abundance. It can be concluded from comparison of the zooplankton abundance plots (Figures 1, 2, 3) and from the relative species abundance plot (Figure 4), that low numbers during winter months are coincident with 1) a decrease in relative abundance of the endemic copepod species and 2) an increase in importance of warmwater species and noncopepod taxa. In addition to copepods with southern affinities, *Oikopleura* spp. and chaetognaths become important during the winter.

There is marked seasonality in the relative abundance of each taxon. This will be discussed station-by-station. At NH 1 *Pseudocalanus* sp. were numerically important during the upwelling season, usually through August. *Acartia clausii* and *A. longiremis* were always important during the autumn after the cessation of upwelling. *Centropages abdominalis* was never a major component after August, with the exception of 1971. *Calanus marshallae* copepodites and nauplii were

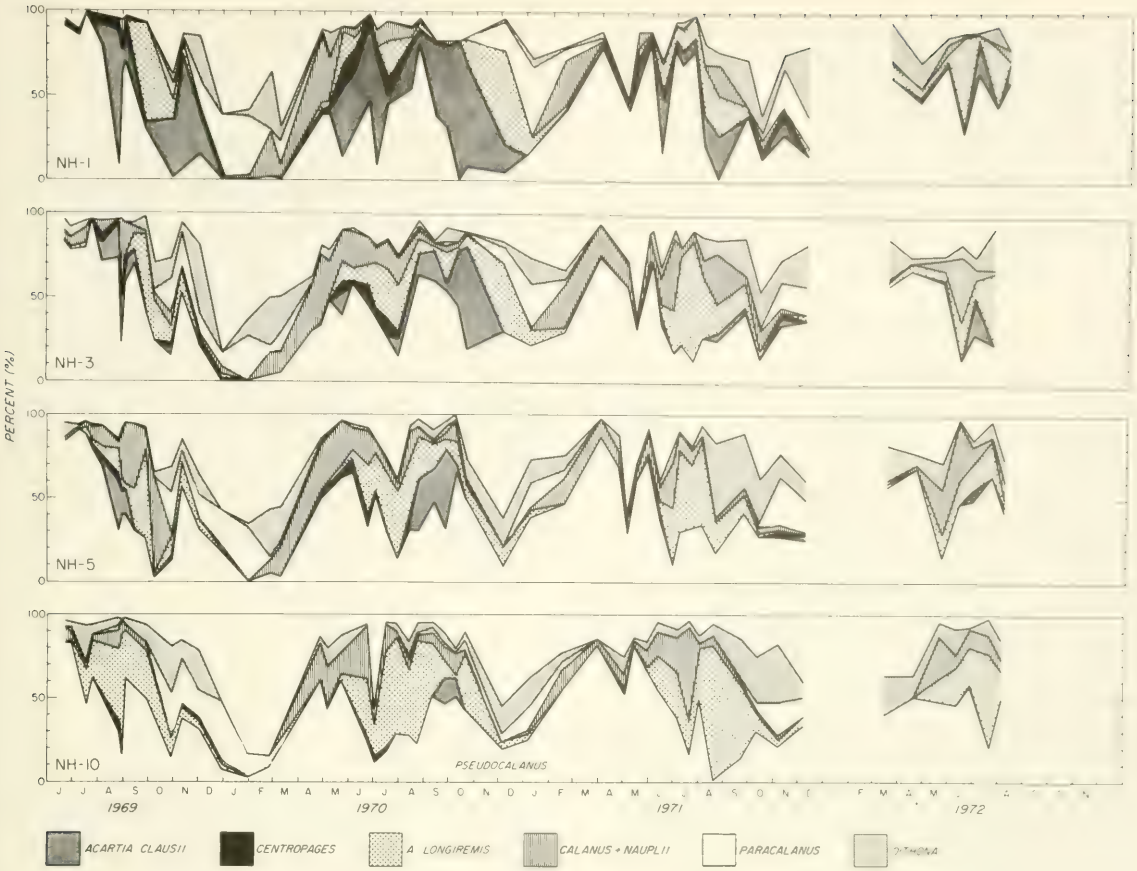

FIGURE 4.—Seasonal cycle of relative abundance (percent of total catch) of the most abundant zooplankton species (all copepods) at stations NH 1, NH 3, NH 5, and NH 10 along the Newport, Oreg., transect over the 3-yr study period. *Centropages* were *C. abdominalis*, *A. longiremis* were *Acartia longiremis*, *Calanus* were *C. marshallae*, *Paracalanus* were *P. parvus*, and *Oithona* were *O. similis*. *Pseudocalanus* sp. are represented by the white area at the bottom of each graph. All remaining zooplankton are represented by the white area at the top of each graph.

most dominant during the spring. *Paracalanus parvus* and *Oithona similis* have their highest relative abundance during the winter.

Different years were different at NH 1, as previously noted (Peterson and Miller 1975). *Pseudocalanus* sp. had a much higher relative abundance during the 1969 and 1971 upwelling seasons than in 1970. During the 1970 upwelling season, *A. clausii* and *Pseudocalanus* sp. shared numerical dominance in many samples. *Centropages abdominalis* was less important during the 1971 upwelling period than in earlier years. *Acartia longiremis* was about equally dominant at various times during all three upwelling seasons. *Oithona similis* was more important during the summers of 1969 and 1971. *Paracalanus parvus* was a significant fraction of the plankton over broader time intervals in 1969 and 1970 than in 1971.

At NH 3 the most striking aspect of the annual cycle compared with NH 1 is the greatly decreased importance of *Acartia clausii* and generally increased importance of *A. longiremis* and *Calanus marshallae*. *Acartia clausii* made up a large fraction of the catch only during October 1970. *Acartia longiremis* and *C. marshallae* were major components over broader intervals in 1970 and 1971 at NH 3 than at NH 1. The annual cycle of *Pseudocalanus* sp. relative abundance at NH 3 was about the same as for NH 1, except for two periods: July of 1970 and 1971. During both times *Pseudocalanus* sp. was dominant at NH 1, whereas *A. longiremis* was dominant at NH 3.

The NH 5 plot is similar to that for NH 3, par-

ticularly between November 1969 and May 1970 and between January and July 1971. Similarly to NH 3, the importance of *A. clausii* is greatly reduced and the importance of *A. longiremis* and *C. marshallae* are increased relative to NH 1. The NH 10 plot follows the NH 5 plot closely during 1970 and 1971 with one exception: in September 1970 *A. clausii* was a significant component at NH 5 but not at NH 10.

DISCUSSION

The annual cycle in the species composition of the zooplankton community along the Oregon coast must result from the annual cycle of the nearshore circulation, which is well described by Huyer et al. (1975). There is an exact correspondence between the sources of currents implied by the direction of flow in each season and the geographic affinities of the species occurring in the water. In summer, when the net water transport is to the south, species with northern affinities dominate. In winter, when transport is northward, species with southern affinities are mixed with the indigenous fauna. Abundances are about an order of magnitude higher in summer than winter, presumably because of production stimulated by coastal upwelling. We term the summer dominants "indigenous" both because they are present throughout the year and because they are the forms which reproduce and complete their life cycles in the Oregon nearshore zone. None of these forms is endemic, however, in that the distributions of all of them extend north around the rim of the Gulf of Alaska and into the Bering Sea. New studies now in progress are intended to describe the distributions within the upwelling ecosystem of the life cycle stages of the summer dominants, and to explain the maintenance of their populations within the system of nearshore currents.

A similar interpretation of seasonal changes in zooplankton species present off Oregon was offered by Cross and Small (1967). They used *Acartia danae* as an indicator of transport from the south (following Frolander 1962), and *Centropages abdominalis* (called *C. mcmurrichi* in their paper) as an indicator of flow from the north. In the present study *A. danae* was very infrequent, and a variety of other species (*Paracalanus parvus, Ctenocalanus vanus, Clausocalanus pergens,* etc.) appear to be much better indicators of southern sources. The studies were different in that the earlier one sampled farther offshore, and it began with the notion that *A. danae* would be an indicator, rather than examining the fauna as a whole.

While there is a generally similar sequence each year in the changes of the copepod species and their abundance, there are also marked differences in these changes between years. These were discussed for the upwelling season by Peterson and Miller (1975). We would like to add to that a brief evaluation of some differences between the winters of our study. Temperature–salinity diagrams including all of the data collected at our inshore stations during the months of October through March are shown in Figure 5. The winter of 1969–70 was warmer than the other winters. Progressive vector diagrams of the winds in each of the winter periods of our study are shown in Figure 6. The winds during 1969–70 were different from those of 1970–71 and 1971–72. During the fall and winter months of 1969–70 there were

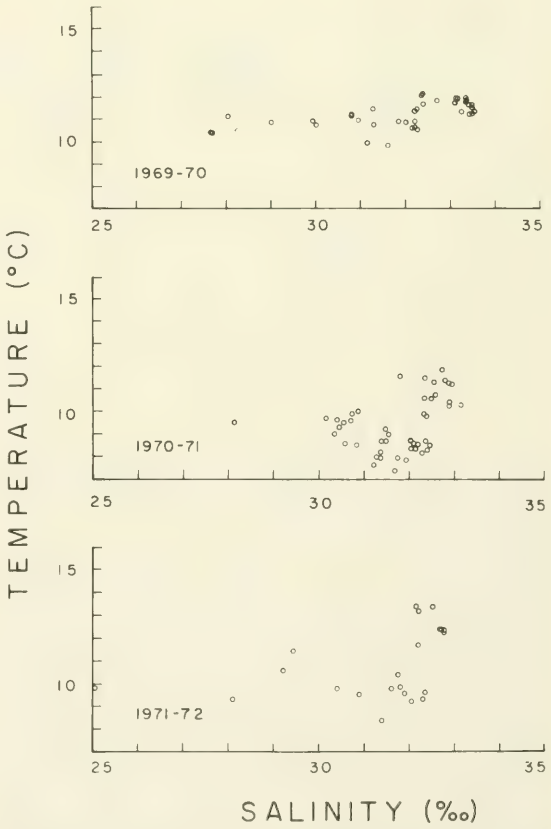

FIGURE 5.—Temperature–salinity scatter diagrams combining data from stations NH 1, NH 3, NH 5, and NH 10 along the Newport, Oreg., transect for the winters of 1969–70, 1970–71, and 1971–72 from October through March.

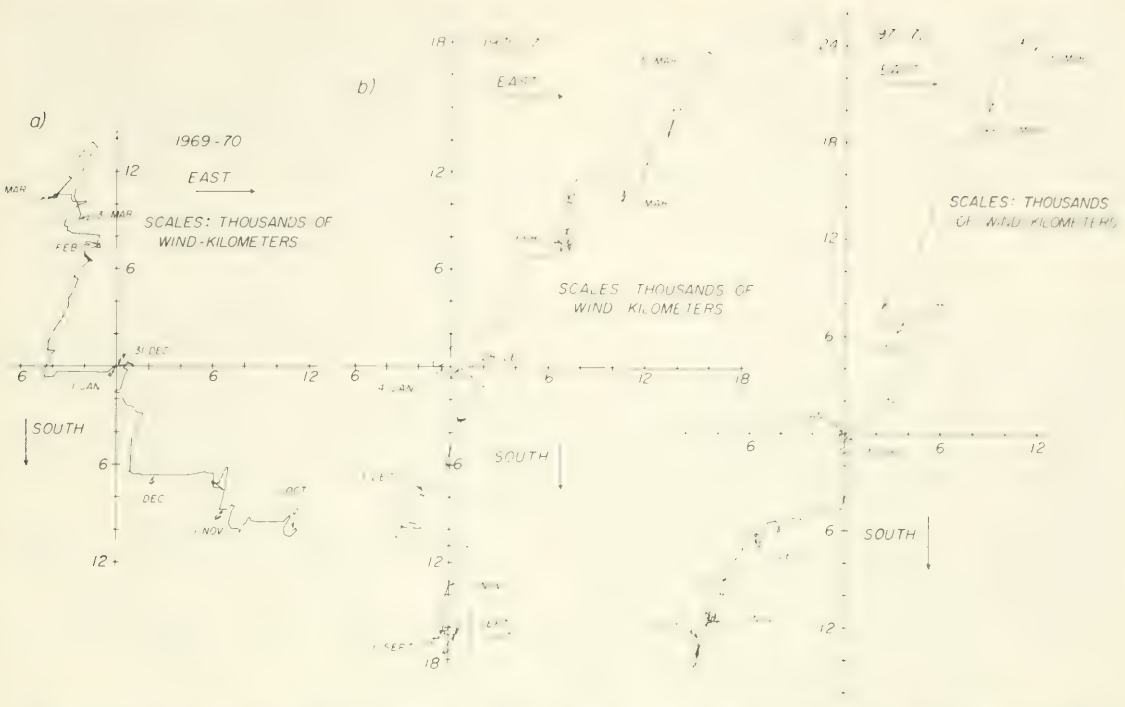

FIGURE 6.—Progressive vector diagrams for the wind at Newport, Oreg., for the winters of 1969–70, 1970–71, and 1971–72.

three intervals with winds from the east: most of October, 23 November to 8 December, and 30 December to 12 January. The entire 6-mo period of winter winds lacked the southwesterly storms that are characteristic of most winters. The other two winter wind patterns shown in Figure 6 are more typical on the basis of comparisons to the winters of later years (1972–73, 1973–74, 1974–75).

Upwelling index data taken from Bakun (1973) for the winters of our study are presented in Table 3. Negative values of the index indicate winds that will produce shoreward convergence of surface waters on the average over the month. Negative values of the anomaly indicate greater-than-usual shoreward convergence. Indices for winter 1969–70 are quite different from those of the other two winters. Onshore convergence was anomalously high in 1969–70 and anomalously low in 1970–71 and 1971–72.

The zooplankton data (see Peterson and Miller (1976) for detailed tabulations) indicate that the northward flow of the Davidson Current probably was much greater in 1969–70 than in the other two years. A number of southern zooplankton species had their greatest abundance during that winter: *Clausocalanus jobei, C. paululus, Oncaea dentipes,* and *O. subtilis*. All of the above 16 copepod species are indicators of water originating south of at least Cape Mendocino, Calif. (Olsen 1949; Fleminger 1964, 1967; Frost and Fleminger 1968).

TABLE 3.—Monthly upwelling index values from Bakun (1973) for midwinter period at lat. 45°N, just north of the Newport, Oreg., transect, during the years of our study.

Month	20-yr mean index for month	1969–70		1970–71		1971–72	
		Index	Anomaly	Index	Anomaly	Index	Anomaly
Nov.	−74	−53	+21	−54	+19	−40	+34
Dec.	−93	−157	−64	−106	−12	−27	+66
Jan.	−94	−98	−4	−32	+62	−19	+75
Feb.	−47	−71	−24	−16	+32	−103	−56
Total			−71		+101		+119

The physical implication of this set of biological observations is that winter periods of gentle winds directly from the south (Figure 6a) are much more effective at moving water northward alongshore than winter periods of violent southwesterly storms (Figures 6b, c), even though the total northward component of the winds during the stormy winters might be much greater. This is in agreement with the temperature results (Figure 5) and with the anomaly in the upwelling indices.

Bakun (1973) pointed out that winters of extreme shoreward convergence of wind-drifted surface waters (negative index anomaly) should cause the density structure to be depressed toward the coast and should accelerate northward flow or decelerate southward flow. "Either situation would favor an anomalous warm advection," according to Bakun.

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GROWTH AND REPRODUCTION OF THE EASTERN SPINNER DOLPHIN, A GEOGRAPHICAL FORM OF *STENELLA LONGIROSTRIS* IN THE EASTERN TROPICAL PACIFIC

WILLIAM F. PERRIN, DAVID B. HOLTS, AND RUTH B. MILLER[1]

ABSTRACT

Estimates of life history parameters for use in assessing status of the population of the eastern spinner dolphin and assessing impact of incidental mortality in the yellowfin tuna fishery are developed from data on 2,675 specimens collected from 1968 to 1975. Average length at birth is 77.0 cm, gestation is 10.6 mo, average length at 1 yr is approximately 134 cm. Three alternative hypotheses of rate of deposition of dentinal growth layers are: I) 1.5 layers/yr throughout life; II) 1.5 layers in the first year, 1/yr thereafter (most favored hypothesis); and III) 1.5 layers until puberty (at 5.5 layers in females and 9 layers in males), and 1/yr thereafter. Males attain sexual maturity on the average at about 170 cm (range 160–195) and 9–12 layers (6.0–11.5 yr), depending on the criterion of testis–epididymis weight chosen. Average length at attainment of social maturity is unknown. Average length of adult males is 174–176 cm. Females on the average attain sexual maturity at 165 cm (5.5 layers or 3.7, 5.0, or 3.7 yr under Hypotheses I, II, and III). Average length of sexually adult females is 171 cm (range 152–187). Ovulation rate is 1/growth layer (1/0.67–1.00 yr) until about 10 ovarian corpora have been accumulated, after which the rate declines. Approximately 1% of adult females are postreproductive. Best estimates of annual pregnancy rate range from 0.450 (based on 1973 data) to 0.474 (based on 1974 data). The pooled estimate for all years' data is 0.461. The corresponding estimates of calving interval (reciprocal of pregnancy rate) are 2.22 yr, 2.11 yr, and 2.17 yr, respectively. Pregnancy rate decreases after age of about 12 layers (8.0, 11.5, or 10.2 yr) concomitant with increase in lactation rate. Overall sex ratio is near parity, but there are about 6% more females than males in adults. Best estimates of gross annual reproductive rate based on the 1973, 1974, and 1975 data are 0.099, 0.103, and 0.105, respectively. The estimate based on pooled data for the 3 yr is 0.102. The estimates are compared with estimates for the spotted dolphin, *Stenella attenuata*, and for other cetaceans.

This paper presents the results of a study of the life history of the eastern spinner dolphin, a geographical form[2] of *Stenella longirostris* (Gray 1828), in the eastern tropical Pacific. The eastern spinner dolphin accounted for the second-highest level of incidental mortality in the purse seine fishery for yellowfin tuna, *Thunnus albacares*, in the eastern Pacific through 1975, after the offshore spotted dolphin, a form of *S. attenuata* (Gray 1846) (Perrin 1969, 1975a; Perrin et al.[3]) The purpose of the study was to develop estimates of life history parameters for use in assessing the status of the eastern spinner dolphin stock and the impact on the stock of incidental mortality in the yellowfin tuna fishery. Preliminary results of partially completed analyses reported here in full appeared in Perrin et al.[4]

Very little previously published information is available on growth and reproduction of the pantropically distributed *S. longirostris*. Cadenat and Doutre (1959) listed body weights and gonadal

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[2]Perrin (1975b) gave the eastern spinner dolphin subspecific rank but stated that the nomenclature is not yet resolved, because the holotype of the species is from an unknown locality. The term "geographical form" is used here as a substitute for the more unwieldy "[*Stenella longirostris*] subspecies (unnamed)." The term "dolphin" is used in conformance with the "list of smaller cetaceans recognized" adopted by the Subcommittee on Smaller Cetaceans, Scientific Committee, International Whaling Commission (Anonymous 1975).

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data for two males (1,940 and 2,040 mm) and two females (1,790 and 1,800 mm) from off Senegal in the tropical Atlantic. Layne (1965) published similar data for two males (1,845 and 1,910 mm) and one female (1,965 mm) from Florida. Pilson and Waller (1970) reported on an adult female of *S. microps* [= *S. longirostris*] 176 cm long, from the eastern Pacific. Harrison et al. (1972) published detailed length, weight, and gonadal data for 12 males (79 to 185 cm) and 21 females (86 to 188 cm) of *S. longirostris* from the eastern Pacific; five males (150 to 182 cm) and two females (169 and 179 cm) of *S. roseiventris* [= *S. longirostis*] from Hawaii; and nine specimens from the eastern Pacific, eight males (165 to 178 cm), and one female (171.5 cm) listed as "probably *S. longirostris*." In their discussion of growth and reproduction, however, they did not differentiate between *S. longirostris* and *S. graffmani* [= *S. attenuata*], a larger species that differs significantly from *S. longirostris* in several features of life history (compare results below with those for *S. attenuata* in Perrin et al. (1976) and Kasuya et al. (1974)).

Several recent reports emanating from the Southwest Fisheries Center, National Marine Fisheries Service (NMFS), NOAA, have dealt with the developmental components of various aspects of the life history of *S. longirostris* other than reproduction. Perrin (1972) described the development of the color pattern in eastern Pacific forms of the species. Perrin and Roberts (1972) analyzed changes in organ weights with size, based on 14 specimens. Dailey and Perrin (1973) described differences in parasite frequencies correlated with age in 19 specimens. Perrin (1975a, b) described developmental variation in morphology in the eastern Pacific and defined three geographical forms (subspecies), of differing adult size: the less-than-2-m-long "eastern spinner," the subject of this report; the slightly larger "whitebelly spinner," found farther offshore; and the "Costa Rican spinner," which is restricted to the coastal waters of Central America and attains a total length of well over 2 m.

This paper treats only the eastern spinner, the form of *S. longirostris* most heavily involved in the tuna fishery through 1975 in terms of numbers of seine net sets and numbers killed (Perrin 1975a). Some data for the whitebelly spinner are included in certain of the analyses of the eastern spinner, including those of length at birth and of brain weight relative to body length, for reasons explained below. A preliminary report on the whitebelly form of *S. longirostris* appeared in Perrin et al.[5]

METHODS AND MATERIALS

The Field Program

Nearly all of the data were collected by NMFS scientific observers aboard commercial tuna vessels. The data collection procedures were the same as previously described for the spotted dolphin (Perrin et al. 1976). Data on *S. longirostris* were collected on 1 cruise in 1968, 4 in 1971, 12 in 1972, 21 in 1973, 33 in 1974, and 30 in 1975. Some specimens were also collected in 1970 by personnel of the Inter-American Tropical Tuna Commission aboard chartered purse seiners.

The Sample

In 1971 and early 1972, when the observer program was very limited, adult female specimens were selected for dissection when available, and the samples for those periods are, therefore, biased with regard to the age and sex structures of the kill. In 1968 and on cruises from October 1972 on, no selection was practiced in determining which animals were to be examined, and those samples are assumed to be cross-sectional with respect to the kill. Fetuses were not collected in 1968.

The sample of animals for which life history data including at least, but not restricted to, sex and body length includes 2,675 specimens, 2,663 from precisely known localities (Figure 1) and 12 from imprecisely known localities, from the eastern tropical Pacific between lat. 21°N and 3°S and west to long. 117°W. Because of the seasonal nature of the tuna fishery, the sample is heavily biased toward the early months of the year, with minimal coverage of the latter part of the year and practically no specimens from the summer months (Table 1). Length-frequency distributions by 5-cm increments for males and females, including fetuses, are presented by year and month in Figures 2 and 3.

[5]Perrin, W. F., D. B. Holts, and R. B. Miller. 1976. Preliminary estimates of some parameters of growth and reproduction of the whitebelly spinner dolphin, a geographical form of *Stenella longirostris*, in the eastern tropical Pacific. Working document submitted to Meeting of Subcommittee on Small Cetaceans, Scientific Committee, International Whaling Commission, London, 7–8 June 1976. SWFC Admin. Rep. LJ-76-12, Natl. Mar. Fish. Serv., NOAA, La Jolla, Calif., 36 p. (Unpubl. rep.)

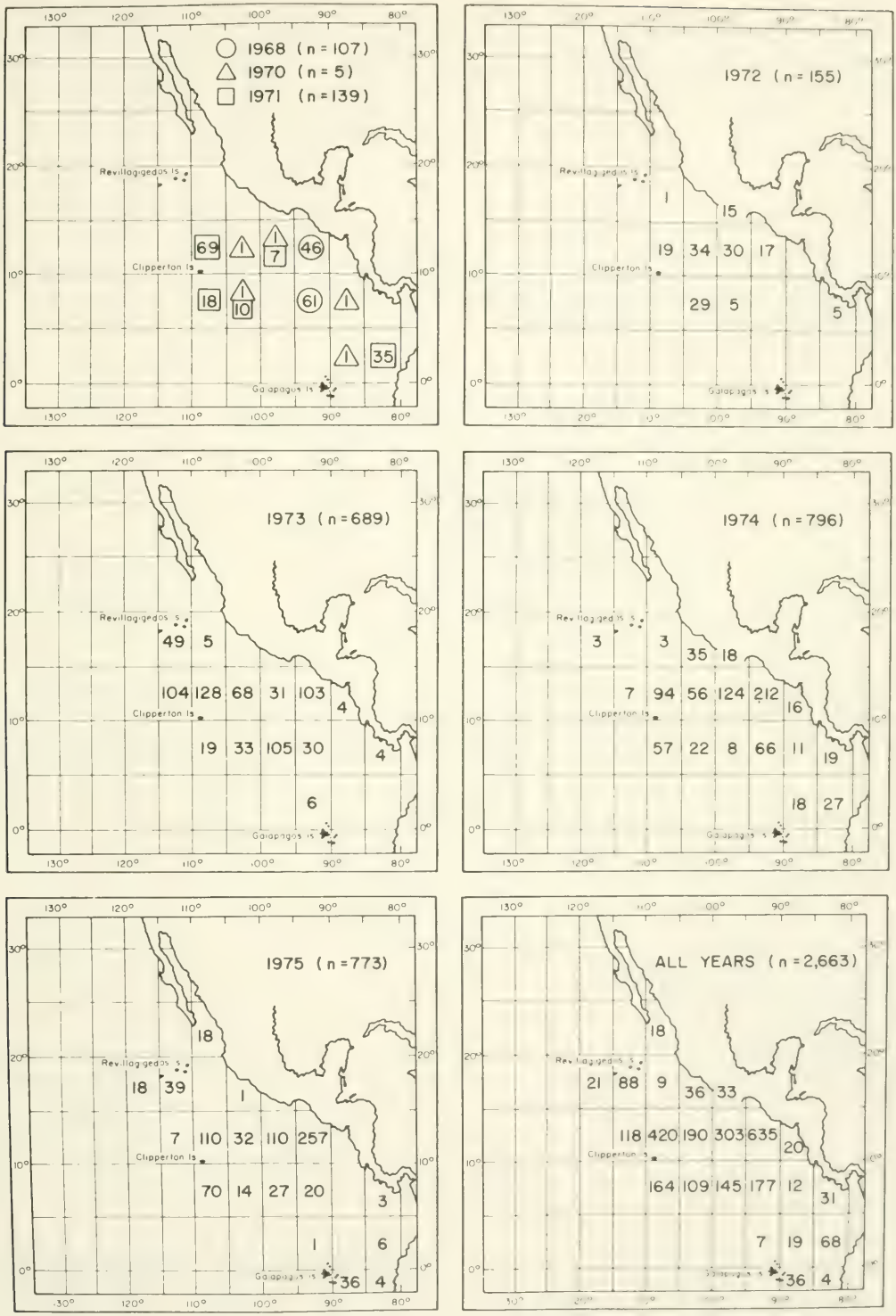

FIGURE 1.—Samples of *Stenella longirostris* collected 1968-75, by 5° square.

TABLE 1.—The sample of eastern spinner dolphins used in the life history analysis, by year and month.

	1968		1970		1971[1]		1972[1]		1973		1974		1975		All years		
Month[2]	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Total
Jan.			1	2	2	11	9	12	23	24	85	104	163	170	283	323	606
Feb.					20	15		15	135	128	230	209	68	72	453	439	892
Mar.							11	35	79	78	26	18	32	31	148	162	310
Apr.	52	55					25	15	50	53	41	30	9	25	177	178	355
May							6	12	1	7	1	3	16	13	24	35	59
June												3	19	21	19	24	43
July			2										16	25	18	25	43
Aug.											3	1	12	12	15	13	28
Oct.							10	7	7	7			17	33	34	47	81
Nov.					35	39			49	45	19	27	12	9	115	120	235
Dec.					6	11			3	3					9	14	23
Total	52	55	3	2	63	76	61	96	347	345	405	395	364	411	1,295	1,380	2,675

[1]In these years, adults were selected (except in Oct. 1972). Fetuses were not collected in 1968.
[2]No samples in September.

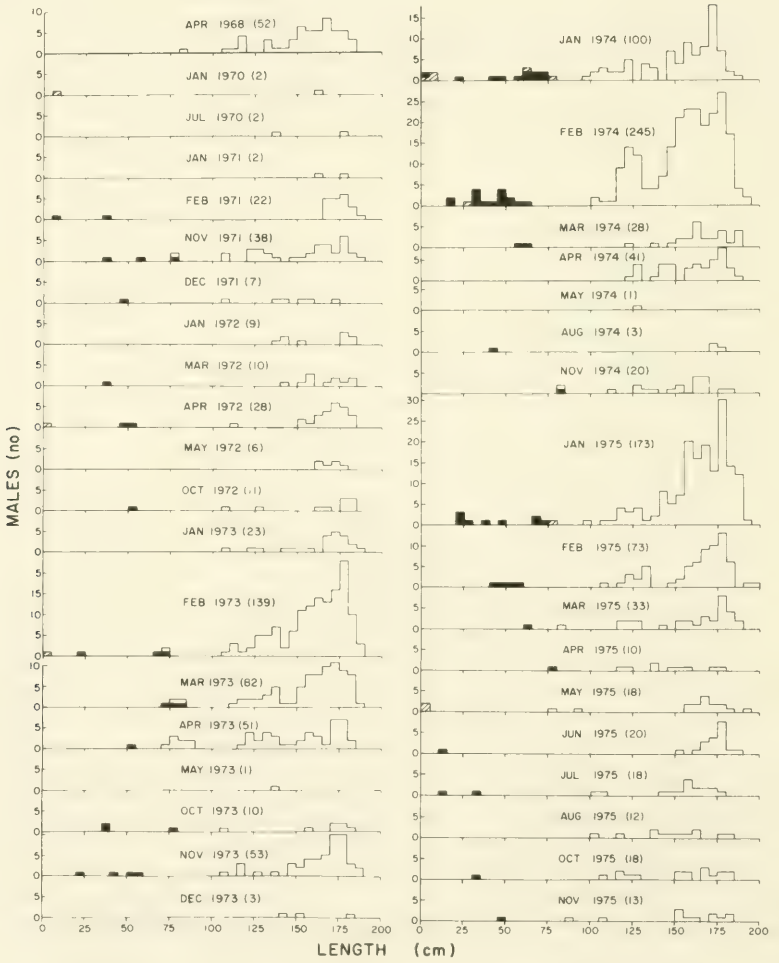

FIGURE 2.—Length-frequency distribution, by 5-cm increments, of collected male eastern spinner dolphins by year and month. Shaded squares are fetuses. Hatched squares are small fetuses of unknown sex (plotted with the males). Sample sizes in parentheses.

Laboratory Procedures

Most laboratory procedures were the same as reported for the earlier study of the growth and reproduction of the spotted dolphin (Perrin et al. 1976). The techniques used in sectioning and reading, however, differed somewhat. Some of the approximately 2,500 teeth prepared (includes recuts, multiple specimens, etc.) were sectioned with multiple cuts, using a high-speed diamond saw

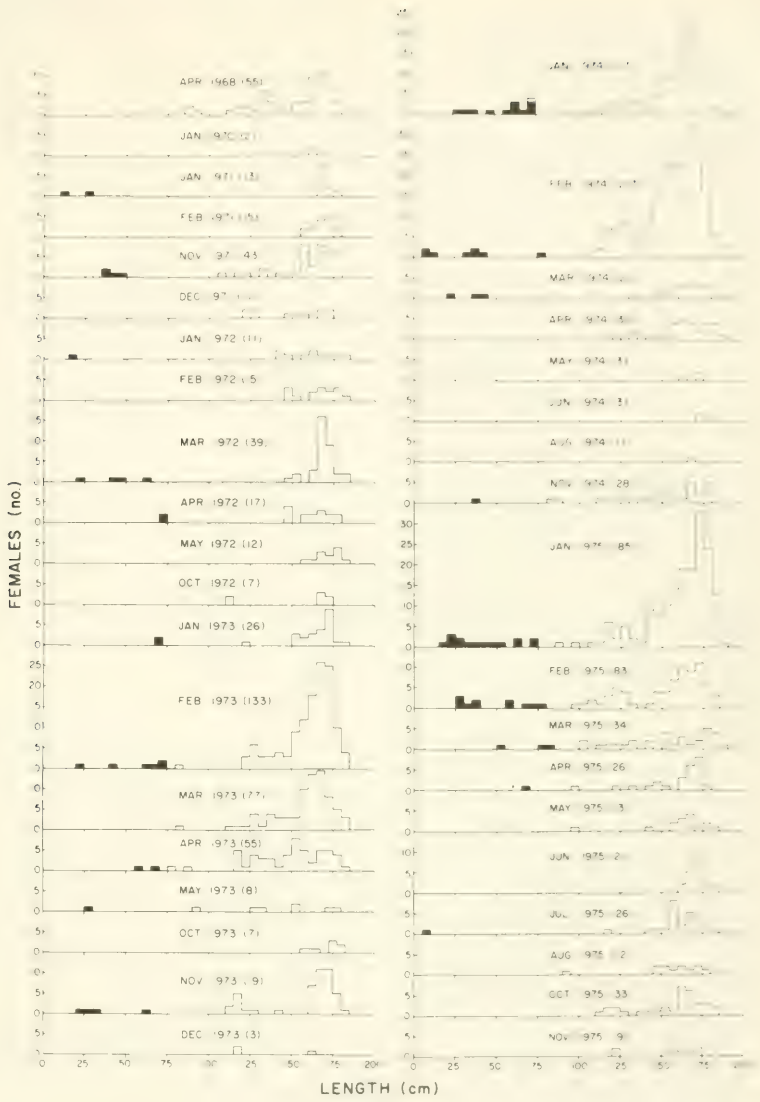

FIGURE 3.—Length-frequency distributions, by 5-cm increments, of collected female eastern spinner dolphins by year and month. Shaded squares are fetuses. Sample sizes in parentheses.

(Felker[6] model 80BQ Hi-speed Precision Cut-off Machine—36,000 rpm) with a single blade, as for *S. attenuata* (Perrin et al. 1976), but most were sectioned with a single cut of tandem blades (yielding a section of uniform 10/1,000-in thickness) with a low speed saw (Isomet model 11-1180 low speed saw—speed variable to 300 rpm). The latter method yielded sections of more uniform thickness and with fewer extraneous surface striations than did the former. After cutting, sections were immediately mounted under coverslips on microscope slides in balsam, omitting the clearing step used for the *S. attenuata* teeth. Our reading and scoring methods also differed from those in the earlier study. We found postnatal dentinal growth to be much more consistent in *S. longirostris* than in *S. attenuata* in pattern of deposition and in readability. No teeth were encountered that did not contain an open cavity, albeit in older specimens a very small one, and a smaller proportion of teeth from younger animals (<12 to 13 layers) contained convoluted secondary dentine than in *S. attenuata*. In the study of *S. attenuata*, growth

[6]Reference to trade names does not imply endorsement of the product by the National Marine Fisheries Service, NOAA.

layers were merely counted to the nearest half layer. In view of the better readability of the *S. longirostris* material, we felt that the approach could be refined. We measured the thickness of each growth layer on an image projected on a 16-cm diameter ground-glass screen attached to a compound microscope using dial calipers accurate to 0.1 mm. The total magnification on the screen was approximately 263 diameters. The first two layers inside the neonatal tooth were measured at approximately the same point along the length for each tooth, about halfway between the proximal end of the neonatal tooth (point where neonatal line meets outer surface) and the distal end of the neonatal pulp cavity. Layers beyond the second were measured at the place along the length of the tooth where they were most clearly defined. In converting measurements to layer units, non-innermost layers beyond the first layer were scored as full layer units regardless of thickness. The first layer, second (when innermost), and subsequent layers (when innermost) were treated differently, as follows:

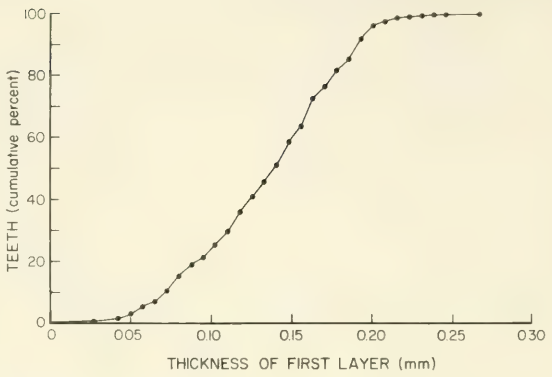

FIGURE 4.—Cumulative percent of first growth layers in relation to thickness of layer in the teeth of 417 eastern spinner dolphins showing asymptote of sigmoid curve at about 0.20 mm.

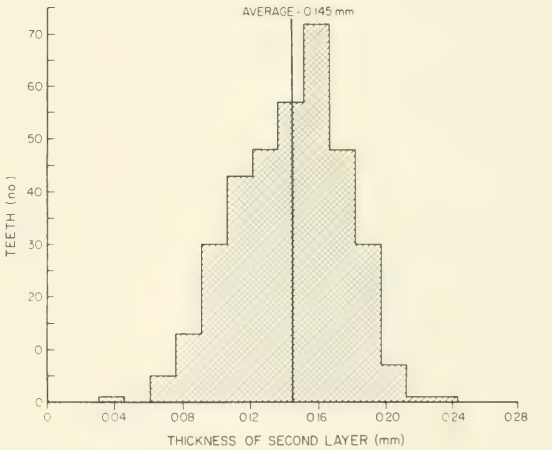

FIGURE 5.—Frequency distribution of thickness of second growth layer in teeth of 361 eastern spinner dolphins.

First Layer

Cumulative percent of 417 first layers measured rapidly approaches an asymptote at approximately 0.20 mm (Figure 4). A first layer 0.20 mm thick or thicker was therefore scored as a full layer unit, and the thickness of a first layer <0.20 mm thick was divided by 0.20 mm to yield a partial layer unit.

Second Layer

In 361 teeth with three or more layers, the second layer averaged 0.145 mm thick with relatively low variance (Figure 5). In teeth with two layers, the second layer was scored as a full layer unit if 0.145 mm thick or thicker. An innermost second layer <0.145 mm thick was scored as a partial layer unit by division of the thickness by 0.145 mm.

Layers Beyond Second Layer

Full layers beyond the second layer averaged more than 95% of the thickness of the next older, adjacent layer, with considerable variation that increased toward the center of the tooth (Figure 6). We assumed, as a reasonable approximation, that complete layers beyond the third are of about the same thickness as adjacent layers, and thickness of the innermost layer in teeth with three or more layers was scored as a proportion of the next older, adjacent layer. Layer scores thus obtained were added and rounded off to the nearest tenth of a layer.

Brain weights were obtained from brains dissected out of freshly thawed heads or whole carcasses of specimens deep frozen at sea aboard tunaboats, except for nine weights for *S. attenuata* (two fetuses, two neonates, and four adults) obtained from George A. Sacher (Argonne National Laboratory, Argonne, Ill., pers. commun.).

Testes were weighed with the epididymes attached.

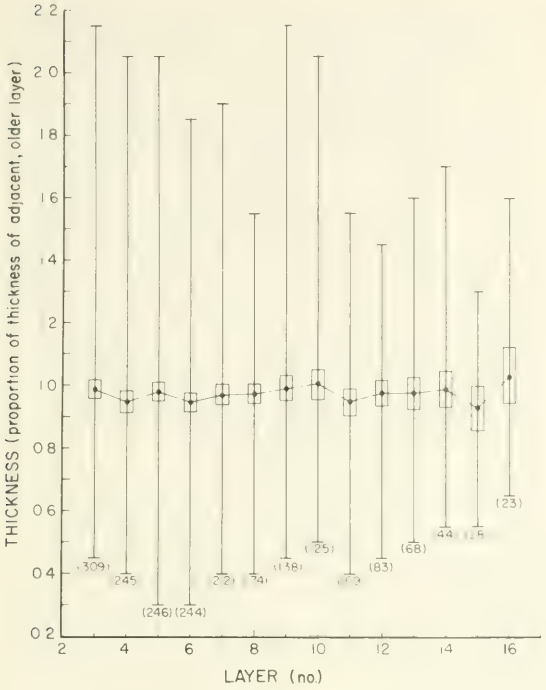

FIGURE 6.—Thickness of growth layers, beyond second postnatal layer, in teeth of the eastern spinner dolphin as proportion of thickness of next older, adjacent zone. Box is one SD on each side of mean; vertical line is range; sample size in parentheses.

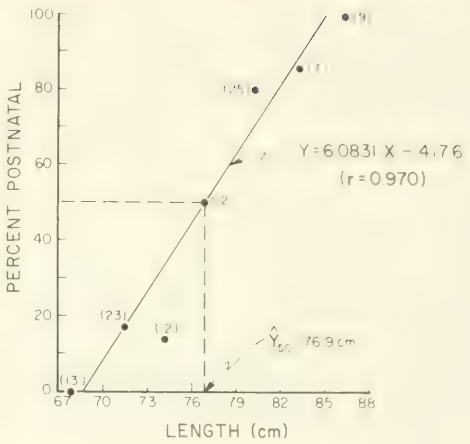

FIGURE 7.—Estimation of average length at birth, based on weighted linear regression of percent postnatal on body length, in 3-cm increments, for 101 specimens of *Stenella longirostris* (54 fetuses and 47 neonates) between 67 and 88 cm long.

RESULTS

Growth

Length at Birth

The largest fetus encountered was 84 cm long. The smallest free-swimming calf was 70 cm long. Estimated average length at birth is 76.9 cm. The estimate is based on a weighted linear regression of percent postnatal on body length, for 3-cm groupings, of 101 specimens (54 fetuses and 47 neonates) between 67 and 99 cm long (Figure 7) collected in random samples. Because of the small sizes of the available samples, 23 specimens of the whitebelly form (11 neonates and 12 fetuses) and 23 specimens unidentified to geographical form (16 neonates and 7 fetuses) were included. This is justified because of the small difference in length of adults of the two forms (<5 cm—Perrin 1975a). Such a difference could be expected to translate into a probable error in the estimate of length at birth, based on the present sample composition, of <0.5 cm, less than that to be expected to be introduced by reduction of the sample size (by 47%) through restriction to specimens known to be eastern spinner dolphins. The estimate is rounded off to 77 cm in analyses below.

This method of estimating average length at birth assumes that pregnant females and calves are 1) equally vulnerable to capture in the purse seine, 2) equally likely to die once captured, and 3) equally represented in the sample of dead animals measured. It also assumes equal rates of prenatal and postnatal natural mortality and assumes that the stresses imposed by pursuit and capture do not cause premature births during the chase or in the net. It was not possible to test these assumptions although some evidence indicates that the last may not be justified (see discussion below in The Calving Cycle and Pregnancy Rate).

Length of Gestation and Fetal Growth

The usual method used to estimate length of gestation is that of Laws (1959), in which progression of a mode in fetal lengths is followed through the seasons. This method was used to estimate length of gestation for the spotted dolphin (Perrin et al. 1976). The method could not be applied to the present samples of data for the eastern spinner dolphin, however. Although breeding is perhaps synchronous at some level (e.g., note peaks in the length–frequency distributions for postnatal males and females in February and April 1973, and February 1974—Figures 2, 3), progression of

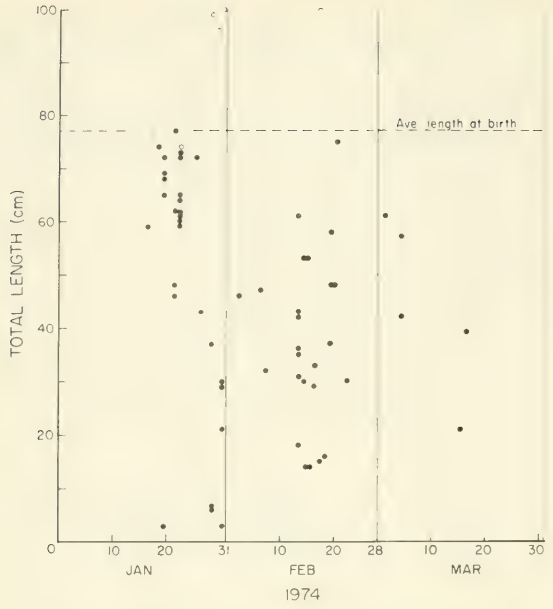

FIGURE 8.—Scatterplot of lengths of fetuses and neonates (open dots) of the eastern spinner dolphin on day of capture, January-March 1974.

fetal modes is not apparent in the data. For example, in the large samples of fetuses collected in January–March 1974 (Figure 8), a sharp mode at 60 to 75 cm in January is not apparent in February, even as neonates, and the diffuse mode at 30 to 60 cm in February is not accounted for in the January sample. A probable reason for these discrepancies is the existence of area-related differences in the timing of calving peaks or in the degree of synchrony of breeding. The tuna fleet, our source of samples, moves around from month to month. The January 1974 samples came for the most part from more easterly, offshore localities than did the February samples (Figure 9). In other words, in 1974, calving in the more offshore region may have been sharply synchronized, with a peak in February–March, while in the more onshore region, calving may have been spread over most of the year. This hypothesis is reinforced by the data for January–April 1975, when sizeable samples of fetuses were collected in the more onshore region during both January and February and smaller samples through April (Figure 10) were from more offshore (around Clipperton Island), northerly

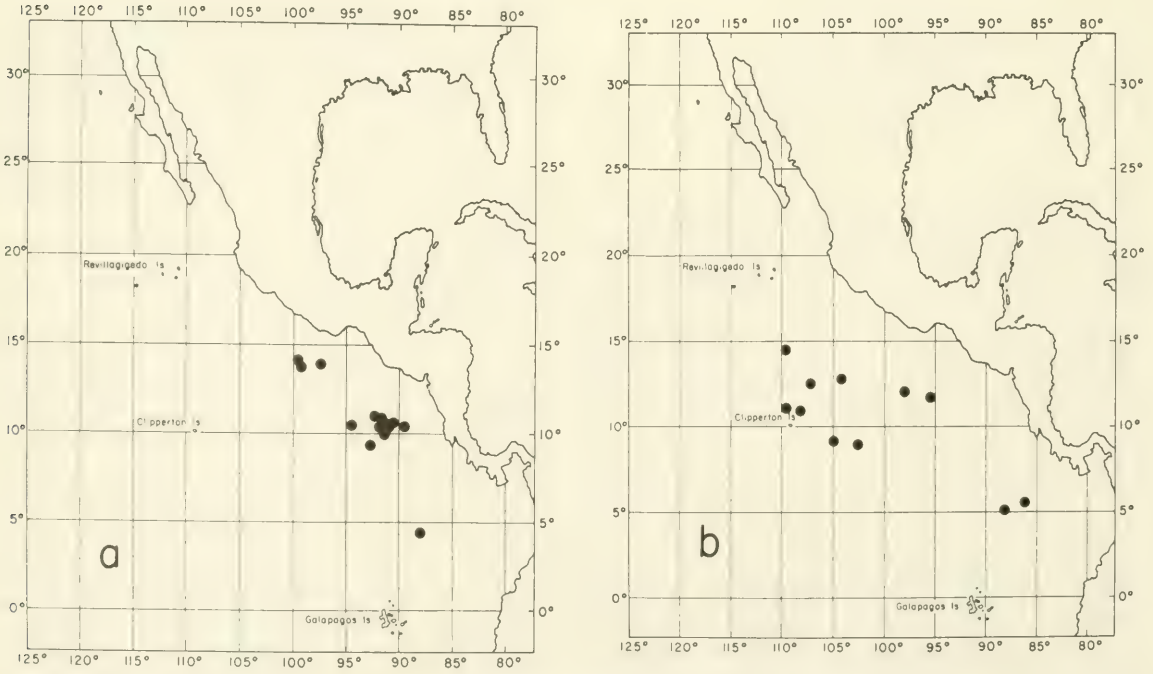

FIGURE 9.—Localities at which fetuses of the eastern spinner dolphin were collected in January (a) and February (b) 1974.

(Revillagigedos Islands), or southerly (near the Equator, east of the Galapagos Islands) regions. Even if only onshore samples are considered (those circled in Figure 10), there is no clear pattern of progression of fetal length modes (Figure 11). It is, of course, possible that the size of the population unit within which breeding is synchronous may be smaller than suggested by the onshore-offshore comparison. In any case, this complexity makes impossible the use of Laws' method for estimating gestation based on aggregated samples, and stratification of the data to even smaller areas than used above yields samples too small for meaningful analysis. For these reasons, we attempted to estimate length of gestation by two other, less direct methods: a) on the basis of relative length at birth compared with that of other, closely related delphinids for which estimates of gestation period exist, and b) on the basis of a recently discovered empirical relationship between brain size parameters and gestation in mammals.

ESTIMATE FROM COMPARISON WITH OTHER DELPHINIDS BASED ON LENGTH AT BIRTH.—Estimates of length of gestation derived by comparable methods are available for four delphinids, sensu stricto (Table 2). There is a positive correlation among these closely related forms between length of gestation and length at birth (Figure 12). Extrapolation of this relationship to

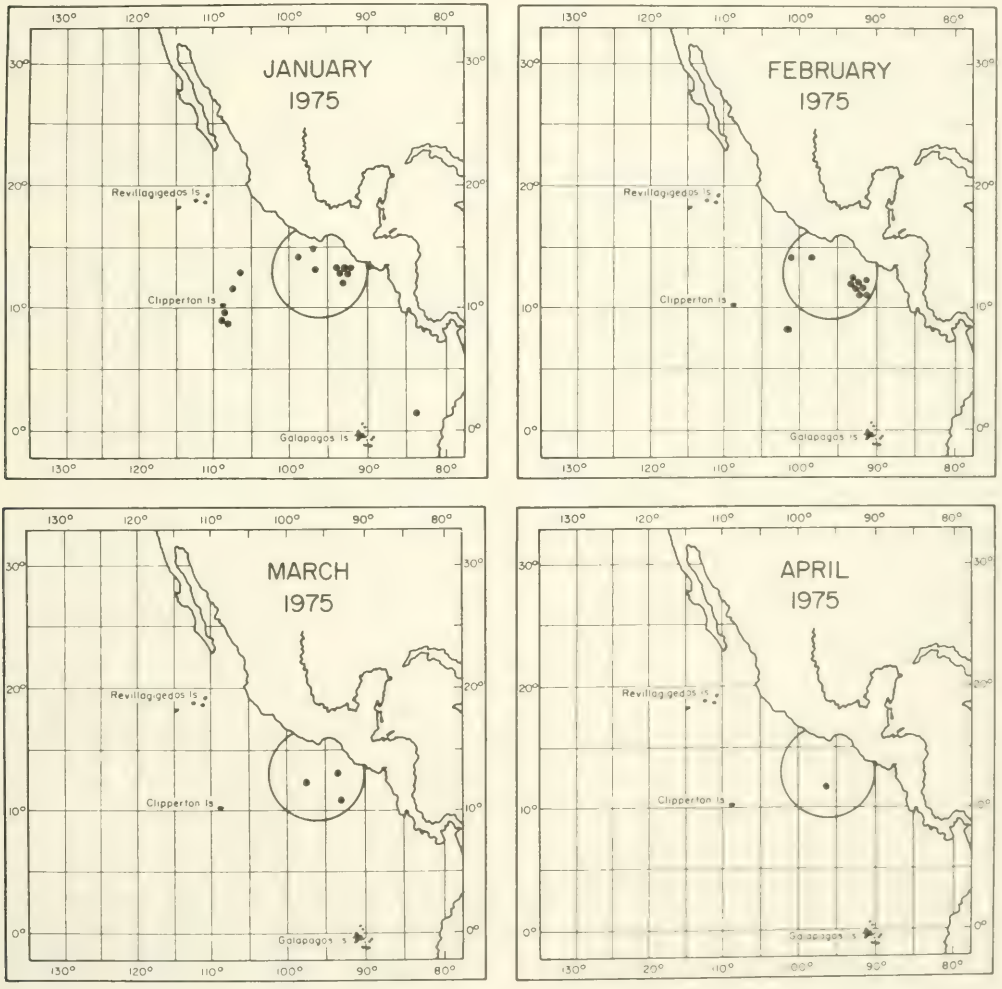

FIGURE 10.—Localities at which fetuses of the eastern spinner dolphin were collected, January-April 1975.

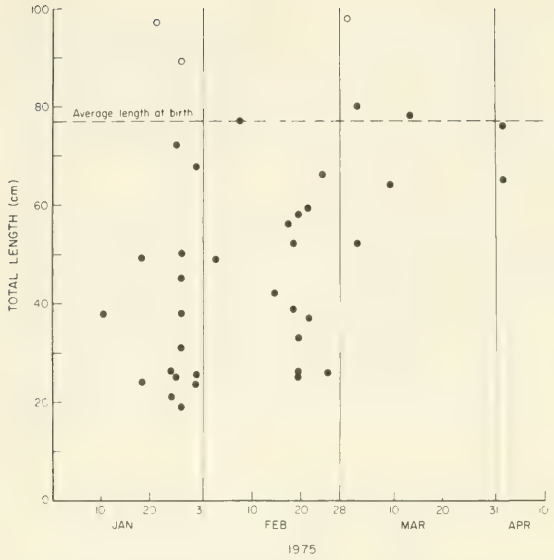

FIGURE 11.—Scatterplot of lengths of fetuses and neonates (open dots) of the eastern spinner dolphin on day of capture, January-April 1975 (specimens from localities circled in Figure 10).

TABLE 2.—Estimated average length at birth and length of gestation in four delphinids. Data for *Globicephala* from Sergeant (1962), for *Tursiops* from Sergeant et al. (1973), for *Stenella coeruleoalba* from Kasuya (1972), for *S. attenuata* from Kasuya et al. (1974) (off Japan) and from Perrin et al. (1976) (eastern Pacific). Common and scientific names follow Subcommittee on Small Cetaceans, Scientific Committee, IWC (Anonymous 1975).

Species	Length at birth (cm)	Gestation (mo)
Long-finned pilot whale *Globicephala melaena* (Newfoundland)	176.0 (average of males and females)	15.75 (15.5-16.0)
Bottlenose dolphin *Tursiops truncatus* (northeast Florida)	100.0	12.0
Striped dolphin *Stenella coeruleoalba* (off Japan)	99.8	12.0
Spotted dolphin *Stenella attenuata*		
a. (off Japan)	89.0	11.2
b. (eastern Pacific)	82.5	11.5

length at birth for *S. longirostris* of 77 cm yields a deduced length of gestation of 10.74 mo (325 days).

ESTIMATE BASED ON GROWTH PARAMETERS OF THE BRAIN.—Sacher and Staffeldt (1974) recently demonstrated an empirical relationship between gestation time and brain weight in placental mammals. This relationship explains more of the wide variation in mammalian gestation times than do previous empirical approaches involving body size parameters, such as cube root

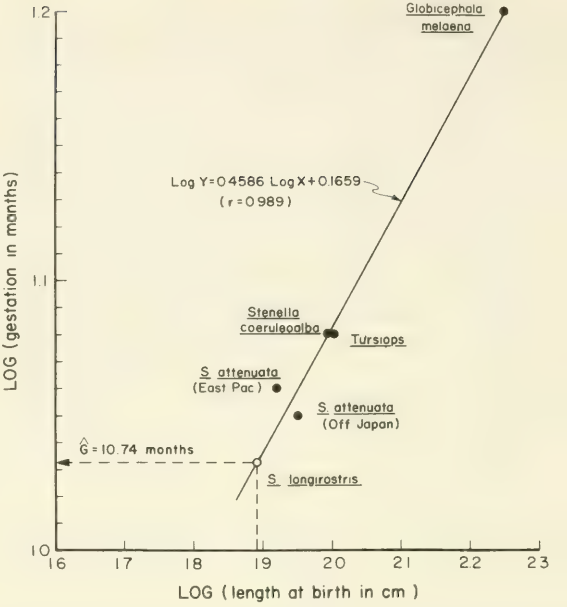

FIGURE 12.—Relationship between log of length of gestation and log of length at birth in four delphinid cetaceans, with extrapolation to predicted length of gestation in the eastern spinner dolphin.

of weight at birth (Huggett and Widdas 1951) or length at birth (as in above estimate). They developed a predictive equation based on linear multiple regression analysis:

$$\log G = 0.274 \log E_n + 0.144 \log A_e + 0.173 \log N + 1.853$$

where G = gestation time in days
E_n = neonatal brain weight in grams
A_e = "brain size advancement," or ratio of neonatal to adult brain weight
N = litter size (1 in cetaceans).

Application of this equation to brain data for *S. longirostris* (Figure 13—neonatal brain weight = 231 g, adult brain weight = 465 g) yields an estimate of gestation time of 286 days (9.45 mo). The method has not yet been tested on a significant number of delphinid species for which gestation time has been more directly estimated,[7] and we

[7]The estimates used by Sacher and Staffeldt of brain weight at birth and adulthood for *Tursiops* are from Lilly (1967) and are based on samples of unstated and probably small size, a very important consideration in light of the large individual variation in these features (Figures 15, 16) and geographical variation in overall size (Anonymous 1975). For example, eight *Tursiops* brain weights summarized by Gihr and Pilleri (1969) averaged

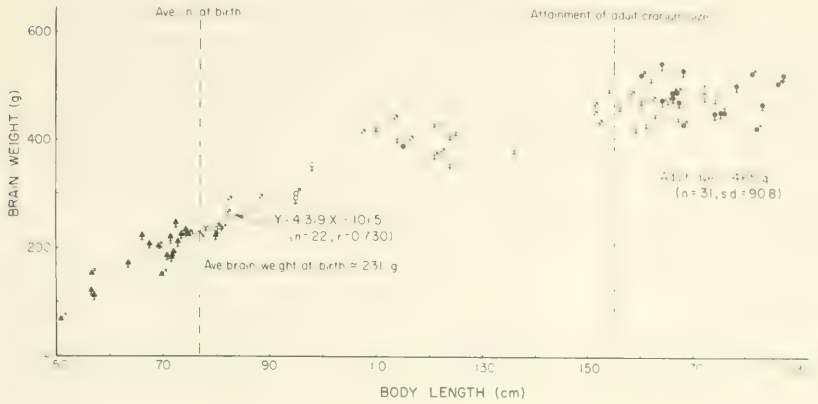

FIGURE 13.—Scatterplot of brain weight on body length for 77 specimens of *Stenella longirostris* from the eastern Pacific. The sample of fetuses and neonates (<100 cm) includes 11 eastern spinner dolphins, 9 whitebelly spinner dolphins, and 9 specimens (mostly fetuses) unidentified to race. Triangles are fetuses, open circles are sexually immature postnatal specimens, shaded circles are sexually adult specimens (by criteria explained in text below). Length at attainment of adult cranium size based on data in Perrin (1975b). The linear regression to estimate brain weight at birth is based on 22 near-term fetuses and neonates 63 to 88 cm long.

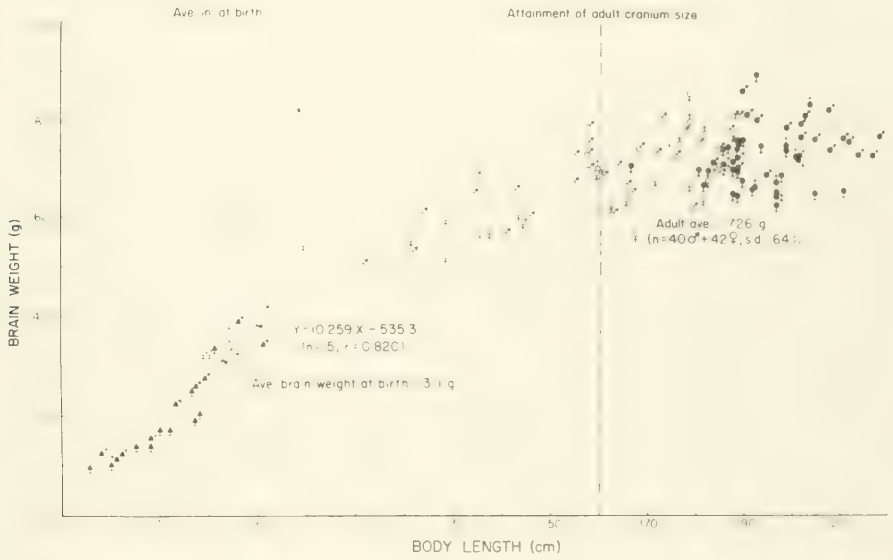

FIGURE 14.—Scatterplot of brain weight on body length for 133 eastern spinner dolphins from the offshore eastern tropical Pacific. Triangles are fetuses, open circles are sexually adult specimens. Linear regression to estimate brain weight at birth based on near-term fetuses and neonates, 73 to 91 cm long. Criteria for sexual maturity and basis for length at attainment of adult cranium size from Perrin (1975b).

1,475 g, compared with the 1,600 g reported by Lilly based on an unknown sample size. Twelve nonneonatal brain weights (probably including some of juveniles) published by Morgane and Jacobs (1972) ranged from 1,260 to 1,950 g and averaged 1,536 g. Thus, deviation of the estimate of Sacher and Staffeldt for *Tursiops* (396 days, or 13.08 mo) from the more directly obtained estimate of 12 mo (Sergeant et al. 1973), an overestimate of about 10%, is of unknown significance and probably reflects statistical error as well as possibly deductive error.

therefore applied the equation to brain data for the spotted dolphin, *S. attenuata* (Figure 14—neonatal brain weight = 311 g, adult brain weight = 726 g). The estimate of gestation time obtained is 304 days, or 10.03 mo, as compared with 11.5 mo (rounded off) estimated by a more direct method

(Perrin et al. 1976). If it be assumed that some factor in delphinid growth is unaccounted for in the Sacher-Staffeldt model and that gestation time for *S. longirostris* is underestimated to a similar degree (11.5 mo minus 10.0 mo/11.5 mo, or 13%), an adjusted Sacher-Staffeldt estimate of 10.54 mo is obtained.

The estimate based on length at birth (10.74 mo) and the adjusted Sacher-Staffeldt estimate (10.54 mo) are close to each other, and a rounded off average of the two estimates, 10.6 mo, is used below in the analyses of reproduction. Making the assumption that fetal growth follows a pattern similar to that in *S. attenuata,* i.e., that t_0 in Laws' fetal growth equation $L = a(t - t_0)$ is approximately the same proportion of gestation time as in *S. attenuata,* or 0.135 t_g (Perrin et al. 1976), a fetal growth curve can be estimated (Figure 15). The slope of the linear portion of the curve is 8.367 cm/mo, as compared with 8.283 cm/mo estimated for *S. attenuata* (Perrin et al. 1976).

Postnatal Growth

We found it impossible to estimate postnatal growth rates by the usual method of following the seasonal progression of length modes, for the reasons discussed above. We deduced an estimate of growth rate during the first 10 to 11 mo by application of the equation, $\log Y = 0.99 \log X - 1.33$, expressing an inferred relationship in toothed cetaceans between length at birth (X above) and the difference (Y above) between the growth rates during the linear phases of fetal and early postnatal growth (Perrin et al. 1976). The predicted difference based on length at birth of 77 cm is 3.60 cm/mo. Subtraction of this from the fetal linear growth (estimated above) of 8.37 cm/mo yields an estimate of average growth rate during the first 10 to 11 mo after birth of 4.77 cm/mo. If this is taken as an estimate of average growth rate during the first year, predicted length at 1 yr is 134 cm. This method overestimates length at 1 yr to some unknown, but slight extent, as growth is only approximately linear in the first year.

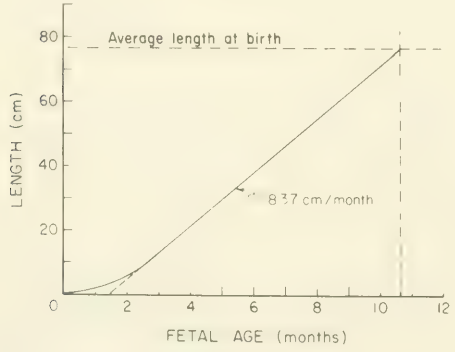

FIGURE 15.—Estimated fetal growth curve for the eastern spinner dolphin.

We examined the relationship between length and number of postnatal dentinal growth layers in the teeth for 183 males and 250 females (Figure 16). The occurrence in the samples of length-layer data for relatively more females than males with more than about 12 layers is accounted for by the fact that the sample of males selected for tooth-sectioning was stratified entirely by length, whereas the sample of females was stratified by length in juveniles and by number of ovarian corpora in adults. All females with more than 10 ovarian corpora were included in the sample, in addition to randomly selected, corpora-stratified subsamples of females with <10 corpora.

We fit growth curves to the data (to single-layer incremental means), using a two-cycle version of the Laird growth model (see Perrin et al. 1976 for discussion of the model). Juvenile males and females were considered jointly. The fit was forced through the origin (zero growth layers, and estimated length at birth of 77 cm), and asymptotic length (L_∞) was estimated as the average length of animals with 13 or more layers (L_∞ for 12 males = 179.46 cm and for 60 females = 170.91 cm), fixing the upper ends of the two curves of the second cycle. The simultaneous iterative fitting procedure arrived at 4.111 growth layers (rounded off to 4 below) as the age at which convergence of the three curves (estimated onset of a secondary growth spurt) yields the best fit (Figure 16). Estimated length at this age is 156.85 cm. The Laird/Gompertz model (Laird 1969) is

$$L(t) = L_0 \exp\left\{\frac{a}{\alpha}\left[1 - \exp(-\alpha t)\right]\right\}$$

where L = length in centimeters
t = age
L_0 = length at age zero
a = specific rate of exponential growth
α = rate of decay of exponential growth.

A form of the model generalized to the present case of more than one cycle is

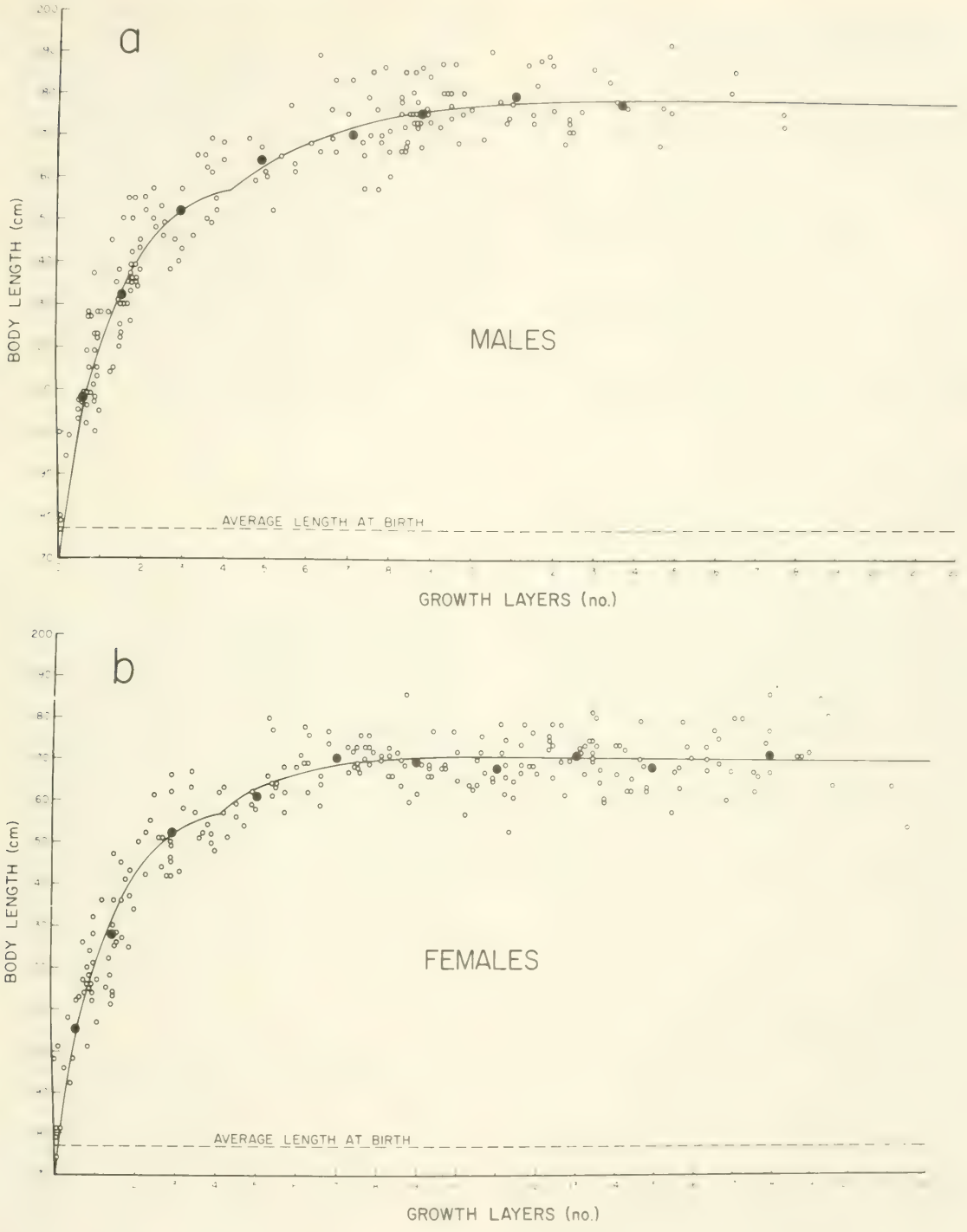

FIGURE 16.—Scatterplot of body length on number of postnatal dentinal growth layers in 183 male (a) and 250 female (b) eastern spinner dolphins. Circled dots are means for 0-1 layer, 1-2 layers, for 2-layer increments thereafter until 12 layers in males and 16 in females and for ≥12 layers and ≥16 layers, respectively. The line is a two-cycle Laird fit to single-layer incremental means (see text).

$$L(t) = L' \exp\left\{\frac{a}{\alpha}\left[1-\exp(-\alpha(t-t'))\right]\right\}$$

where L' = length (centimeters) at start of cycle
t' = age (growth layers) at start of cycle.

The growth equation for juveniles of <4 growth layers is

$$L = 77 \exp\left\{\frac{0.6630}{0.9098}\left[1-\exp(-0.9098t)\right]\right\}.$$

The growth equation for males of >4 growth layers is

$$L = 156.85 \exp\left\{\frac{0.0507}{0.3765}\left[1-\exp(-0.3765(t-4.11))\right]\right\},$$

and for females

$$L = 156.85 \exp\left\{\frac{0.0546}{0.6354}\left[1-\exp(-0.6354(t-4.11))\right]\right\}.$$

The fits of the model to both males and females is excellent, albeit slightly better for the females about the point of convergence of the two curves than for males.

The equations rearranged and reduced for estimating age from length are

♂ and ♀ < 157 cm

$$t = -1.099 \ln(6.960 - 1.372 \ln L)$$

♂ > 157 cm

$$t = 4.113 - 2.656 \ln(38.540 - 7.426 \ln L)$$

♀ > 157 cm

$$t = 4.113 - 1.574 \ln(59.871 - 11.645 \ln L).$$

Note: These equations should not be used to estimate age from actual length data except for grouped samples of smaller animals (about 165 cm or less in females and 170 cm in males), for which growth rate is still large compared with individual variation in length.

Estimated age in growth layers at 134 cm, the predicted length at 1 yr derived above from extrapolative comparison with other delphinids, is 1.57 layers. Since, as discussed above, the estimate of 134 cm is likely to be a slight overestimate due to some nonlinearity of growth during the first year, the estimate of 1.57 layers is rounded down (to the nearest half layer) to 1.5 layers for use below in the various hypotheses of rate of accumulation of layers.

It appears that, effectively, in terms of the data yielded by the tooth readings, 1.5 layers are laid down in the first year. One possible explanation alternative to that of actual deposition of 1.5 layers/yr is that a single layer is laid down in the first year, but that in some individuals (about half) there is a strongly developed subsidiary line within the layer that makes the single layer appear like two layers, yielding an average of 1.5 layers. This explanation seems unlikely, however, in view of the data on thickness of the first layer.

The "subsidiary line" hypothesis would predict a subsidiary inflection or plateau in the cumulative percent of first layers in relation to thickness, and such is not apparent (Figure 4).

We found no correlation between thickness of the innermost growth layer and month of capture (Table 3). It is apparent from the data that the layers are formed rapidly (very few relatively thin innermost layers are seen) and probably throughout the year in the population.

With no basis for direct calibration, we provisionally use three alternative hypotheses of rate of layer deposition (similar to those put forth for the spotted dolphin, *S. attenuata*—Perrin et al. 1976) in the age-based analyses below, namely:

I. One and one-half layers per year, or

TABLE 3.—Thickness of innermost growth layer in teeth of 331 eastern spinner dolphins, with 3-12 layers, by month of capture.

Month	Sample size (no.)	Thickness of innermost layer ÷ thickness of next youngest layer: Average (%)	Minimum (%)	Maximum (%)
Jan.	38	90.1	65	100
Feb.	107	83.3	20	100
Mar.	42	88.3	30	100
Apr.	13	81.1	50	100
May	9	89.9	67	100
Aug.	3	98.0	94	100
Oct.	7	71.1	47	100
Nov.	26	83.6	44	100
Dec.	5	94.0	73	91

II. One and one-half layers in the first year and one per year thereafter, or
III. One and one-half layers per year until puberty (at about nine layers in males and five to six layers in females) and one per year thereafter.

There is a rapidly increasing body of evidence (Perrin et al. 1976; Best 1976) that most delphinids accumulate growth layers at the rate of 1/yr, making Hypothesis II the most likely true of the three, but some uncertainty still exists, especially for tropical forms. We therefore express the conclusions of all age-based analyses below in terms of the three hypotheses. Other, more complex hypotheses can be suggested, but these three in our view probably include the truth.

Reproduction

The Male

Spermatogenesis is histologically evident in 50% of (right) testes weighing 94 g or more (weight of epididymis included) (Figure 17). A perhaps better criterion of sexual maturity is presence of sperm in the epididymis (Figure 18). Combined testis-epididymis weight at which half the males possess "some" or "copious" sperm in the epididymis is approximately 150 g. Another epididymal criterion can be defined, namely, the testis-epididymis weight above which the proportion of males having "copious" sperm in the epididymis does not increase, in this case above 50% at about 400 g. The three testis-epididymis weight criteria of 94 g (50% spermatogenic), 150 g (50% with sperm in epididymis), and 400 g (asymptotic weight with respect to proportion with copious sperm) are considered below in relation to body length and age (in dentinal growth layers).

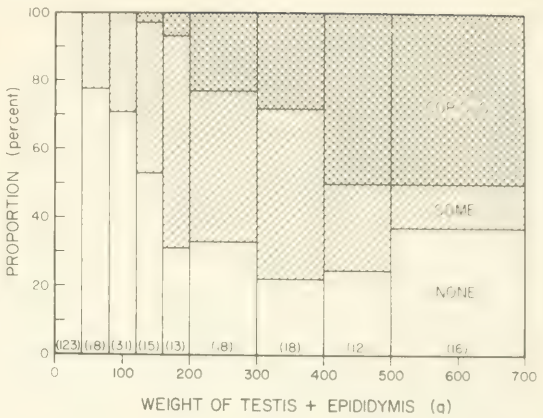

FIGURE 18.—Presence of sperm in epididymis in relation to testis-epididymis weight in the eastern spinner dolphin. Sample sizes in parentheses.

Testis-epididymis weight on the average increases precipitously with body length between 160 and 170 cm (Figure 19), but is only weakly correlated with body length beyond 175 cm. Males of any length above 160 cm can be mature or immature under each of the three criteria defined above. The proportion of males mature under the three criteria stabilizes at about 170 to 175, 175 to 180, and 180 to 185 cm body length, respectively (Figure 20). The average length of adult males under the three criteria ranges from 174 to 176 cm (Table 4).

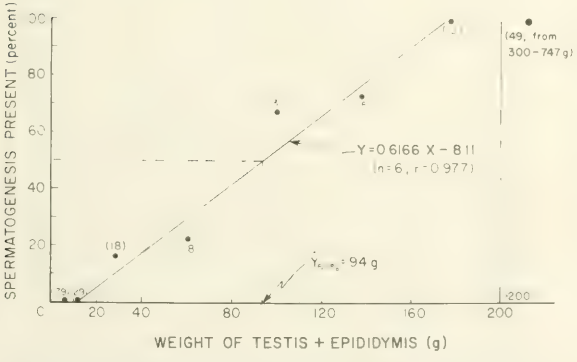

FIGURE 17.—Linear regression analysis of relationship between proportion of males spermatogenic and testis-epididymis weight in the eastern spinner dolphin. Sample sizes in parentheses.

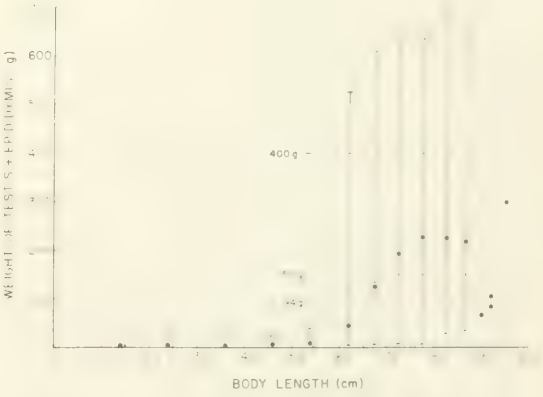

FIGURE 19.—Relationship between testis-epididymis weight and body length in the eastern spinner dolphin. Circled dots are sample means. Vertical bars are ranges. Sample sizes in parentheses.

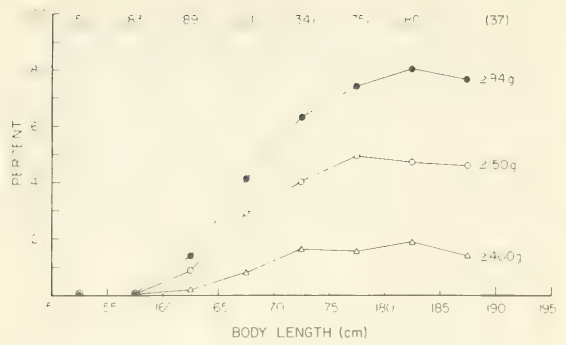

FIGURE 20.—Proportion of males sexually mature in relation to body length in the eastern spinner dolphin under three criteria of testis-epididymis weight. Sample sizes in parentheses.

TABLE 4.—Body length of adult male eastern spinner dolphins under three criteria of sexual maturity.

Weight of testis and epididymis (g)	Sample size (no.)	Body length (cm)			
		Minimum	Maximum	Average	SD
<94	594	108	192	—	—
≥94	356	160	195	176.0	5.99
≥150	230	160	195	175.8	6.06
≥400	81	162	190	174.1	5.79

Testis-epididymis weight is more closely correlated with age (in dentinal growth layers) than with body length (Figure 21). The 94-g level is reached on the average at about 9 growth layers and attained by all males with more than 12 layers. The 150-g level is reached at about 10 layers on the average and by all males at about 13 layers. The 400-g level is reached on the average at about 12 layers, but the oldest male examined (16.5 layers) had a testis-epididymis weight of only 333 g. Estimated average age in years at sexual maturity under the three criteria and under the three layer/year hypotheses ranges from 6.0 to 11.5 yr (Table 5), with the most likely estimates (Hypothesis II) 8.5 to 11.5 yr.

The question of age at attainment of social maturity (sense of Best 1969) in the spinner dolphin must await studies of social structure and breeding patterns. Other (larger) odontocetes, such as the sperm whale, *Physeter catodon,* and the long-finned pilot whale, *Globicephala melaena,* are known or thought to be polygynous, to varying degrees, but the social structure of the spinner dolphin is as yet unknown.

No systematic seasonal variation in testis weight or condition was detected, although the heavy bias in seasonal coverage of the sample precludes an adequate evaluation of this factor.

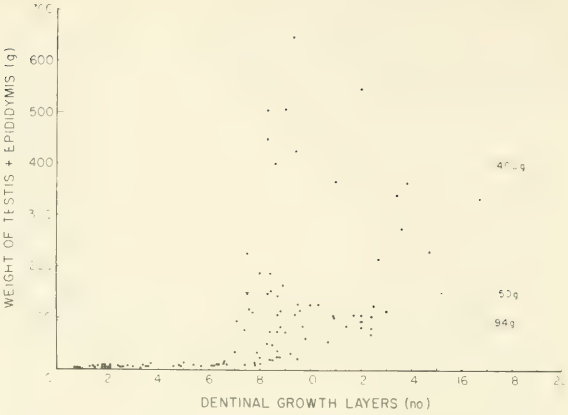

FIGURE 21.—Scatterplot of testis-epididymis weight on age (in dentinal growth layers) for 106 eastern spinner dolphins.

TABLE 5.—Estimated average age in years at attainment of sexual maturity in male eastern spinner dolphins under three criteria of maturity and three growth layer hypotheses.
[See text for definition.]

Testis-epididymis criterion (g)	Age (years) under growth layer hypotheses		
	I	II	III
94	6.0	8.5	6.0
150	6.7	9.5	7.0
400	8.0	11.5	9.0

The Female

ATTAINMENT OF SEXUAL MATURITY.—The smallest sexually mature female in the present sample was 152 cm long. The largest immature female was 182 cm long. One estimate of average length at attainment of sexual maturity is the length at which 50% of the females show evidence of having ovulated, i.e. possess ovaries with one or more scars (corpus luteum or corpus albicans). This length in the present sample of eastern spinner dolphins is estimated at 164.1 cm (Figure 22).

The sigmoid curve in Figure 22 is slightly asymmetrical, that is to say, there are more immature animals (91) above the 50%-mature length of 164.1 cm than there are mature animals below it (62). At 165 cm, the numbers are 80 and 77, respectively. This length, 165 cm, is used below to classify as sexually mature or immature specimens for which ovarian data are lacking. The predicted number of growth zones (from the growth equation) at this length is 5.5.

Average age at attainment of sexual maturity can also be estimated directly from the smaller sample of females for which teeth were sectioned (n = 247). This analysis (Figure 23) estimates

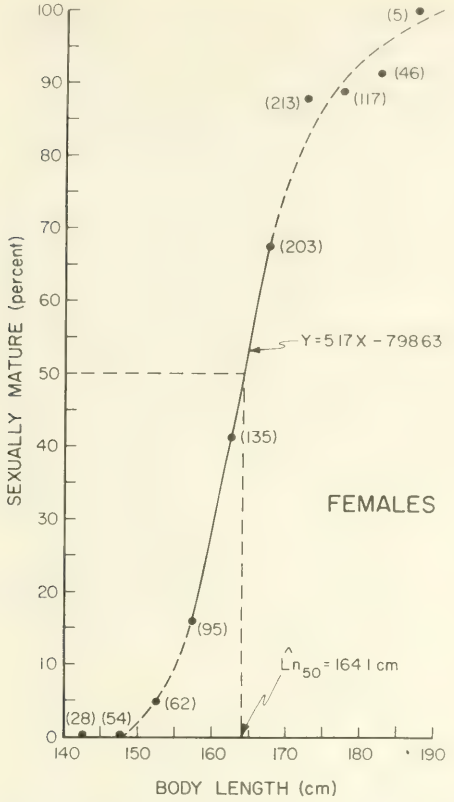

FIGURE 22.—Estimation of body length at which 50% of female eastern spinner dolphins show ovarian evidence of sexual maturity (one or more scars). Fit to central portion of curve (solid line) is linear regression. Dashed portions of curve fitted by eye. Sample sizes in parentheses.

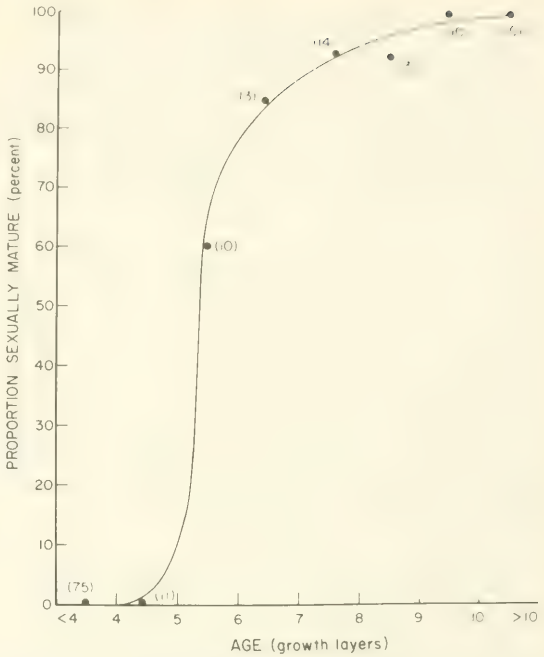

FIGURE 23.—Relationship between proportion of females sexually mature and age, in dentinal growth layers, in the eastern spinner dolphin. Fit is by eye.

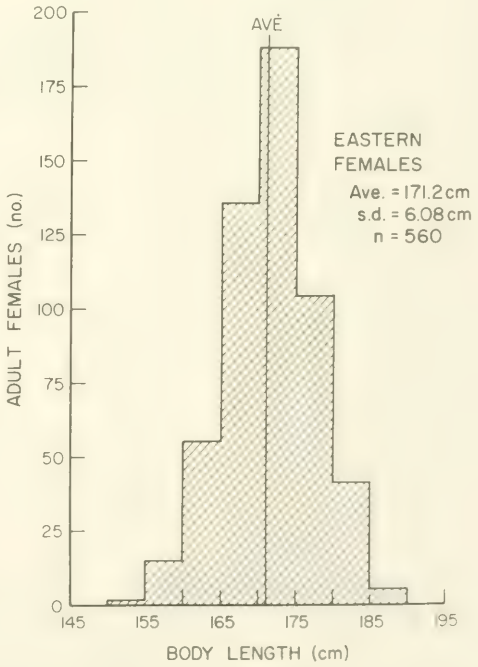

FIGURE 24.—Length-frequency distribution of 560 sexually adult (possessing at least one ovarian corpus) female eastern spinner dolphins.

average age at attainment of maturity at about 5.4 growth layers, in close agreement with the estimate derived from the age/length equation. A rounded-off average of 5.5 layers is used below. Average age in years at attainment of maturity under the three hypotheses of layer deposition rate are 3.7, 5.0, and 3.7 yr, respectively, with the second estimate being most probably correct.

Sexually adult females in the sample ranged from 152 to 187 cm and averaged 171.2 cm in length (Figure 24).

DISTRIBUTION OF CORPORA TO LEFT AND RIGHT OVARIES.—As in all other odontocetes so far studied, the left ovary predominates in ovulation. As in the case of *S. attenuata*, the distribution between left and right side (Table 6) can be accounted for by assuming that about 90 to 95% of the females ovulate the first time from the left ovary, and the remainder from the right, and that

TABLE 6.—Location of corpora (corpora lutea and corpora albicantia) in ovaries of 556 eastern spinner dolphins.

Corpora (no.)	Sample size (no.)	Location of corpora		
		Left ovary only (%)	Right ovary only (%)	Both ovaries (%)
1	41	92.7	7.3	—
2	51	78.4	9.8	11.8
3	50	92.0	2.0	6.0
4	43	90.7	2.3	7.0
5	56	91.1	3.6	5.3
6	53	86.8	11.3	1.9
7	60	85.0	15.0	0.0
8	39	82.1	10.3	7.6
9	26	80.8	11.5	7.7
10-11	63	73.0	19.0	8.0
12-15	55	41.8	1.8	56.4
16-19	13	23.1	0.0	76.9
20-26	6	16.7	0.0	83.3

succeeding ovulations are from the same ovary (left or right) about 90 to 95% of the time. When about 10 corpora have accumulated, emphasis shifts sharply to the opposite ovary.

OVULATION RATE.—The number of ovarian corpora, including corpora lutea, ranged from 1 to 26 in 555 sexually adult females. The frequency distribution (Figure 25) is very similar in shape to that for *S. attenuata* (Perrin et al. 1976) with highest frequencies at 5 to 7 corpora and a sharp falloff after about 10 corpora.

Size-frequency distribution of the various types of corpora albicantia among the corpora-type categories relative to total number of corpora were the same in this sample as in the sample of *S. attenuata* previously studied (Perrin et al. 1976) leading us to believe that, for this species also, corpora of ovulation persist throughout the life of the animal, accumulating at Type 3.

Scatter in a plot of number of corpora on age in growth layers is wide (Figure 26) but not as great as encountered in a study of *S. attenuata* (Perrin et al. 1976). Factors producing the scatter are 1) error in reading growth layers, 2) individual variation in ovulation rate, and 3) change in ovulation rate during the reproductive span. The teeth of *S. longirostris* in this study had more clearly defined, more easily readable growth layers than did those of *S. attenuata* in the previous study, and this probably accounts for the relatively less scatter for the former, although less influence by either or both of the other two factors cannot be ruled out.

Calculation of average ovulation rates from the data in Figure 26 must take into account individual variation in age at first ovulation. The data were grouped into 2-layer intervals (all those with 12 or more layers were included in a single final increment), and average reproductive age by interval P calculated as

$$\bar{A} = \frac{\sum_{i=1}^{P} a_i b_i}{c_i}$$

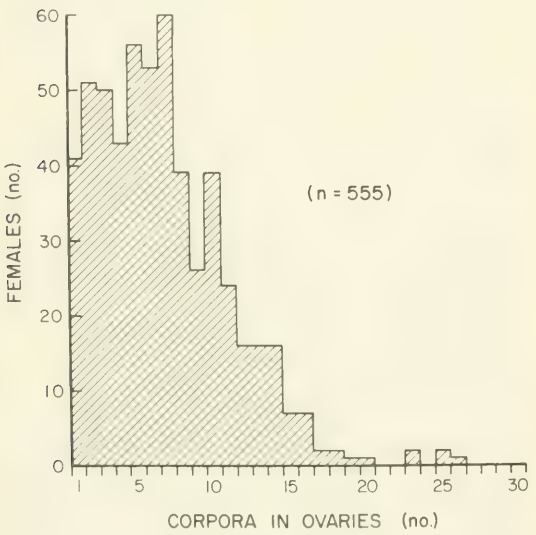

FIGURE 25.—Frequency distribution of ovarian corpora count in 555 female eastern spinner dolphins.

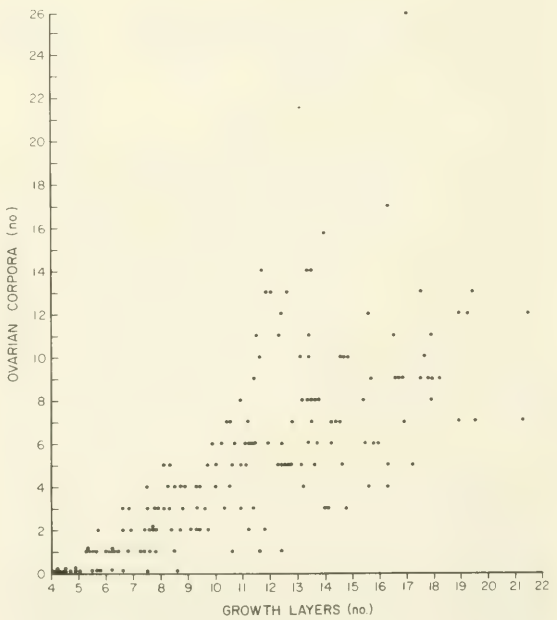

FIGURE 26.—Scatterplot of number of ovarian corpora on age, in dentinal growth layers, in 1,972 female eastern spinner dolphins.

where a_i = percent maturing in ith interval (percent maturing in i minus percent maturing in $i - 1$)
b_i = average reproductive age in interval P of females maturing in i
c_i = percent mature in interval P.

Average reproductive age in the ith interval of females maturing in i was set at 0.50 layer. A plot of number of ovulations on average reproductive age (Figure 27) shows linear increase, with a slope of unity (one ovulation per layer), in number of corpora until about 10 corpora have been accumulated at about 10 layers of reproductive age (15.5 layers total age on the average) when the ovulation rate apparently drops sharply. This is very different from the results obtained in a similar best-fit analysis for *S. attenuata* (Perrin et al. 1976), which indicated average ovulation rates of about four during the first layer, two during the second, and about one per layer thereafter. A power fit to the data for *S. longirostris* (Figure 27) shows much less variation in ovulation rate with age. It appears that in the presently sampled population of *S. longirostris* there is less multiple infertile ovulation in very young mature females than in the studied population of *S. attenuata*. This may be an inherent difference or may reflect differential status of the two populations with respect to exploitation. For example, females could on the average become sexually mature at an earlier age in an exploited population but be less fertile, in terms of pregnancies per ovulation, than had they become mature at greater age. Estimated ovulation rates were higher in the studied eastern Pacific population of *S. attenuata* than in a relatively unexploited population of the same species in Japanese waters (Perrin et at. 1976).

POSTREPRODUCTIVE FEMALES.—Four adult females of 536 examined (≃1.0%) showed clear evidence of being postreproductive, or "senile," by criteria of 1) being inactive, or "resting" (neither pregnant nor lactating); 2) having high corpora count (≥10); 3) having small, withered ovaries (weighing <3.5 g); 4) having no developing follicles (largest follicle <1 mm in diameter); and 5) having no Type 1 or 2 corpora albicantia (terminology of Perrin et al. 1976), indicating recent ovarian activity (Figure 28).

THE CALVING CYCLE AND PREGNANCY RATE.—The calving cycle, for purposes of analyzing the types of field data available, can be divided into three phases: 1) pregnancy, 2) lactation, and 3) "resting"—a catch-all "phase" for animals neither pregnant nor lactating, which includes

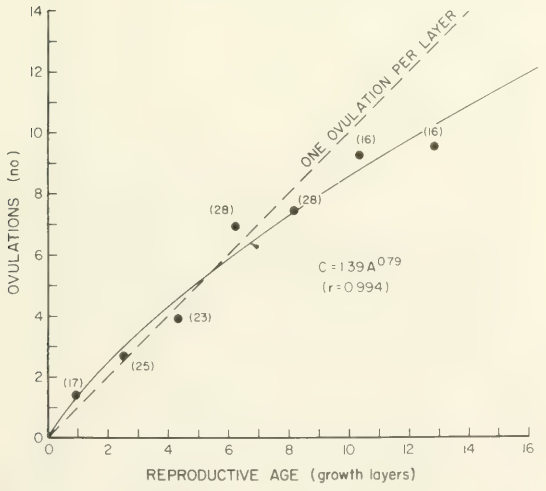

FIGURE 27.—Scatterplot of 2-layer means (last mean is for 12-16 layers) of average number of ovulations on average reproductive age in growth layers in the eastern spinner dolphin. Regression line is power fit. One-ovulation-per-layer line added. Sample sizes in parentheses.

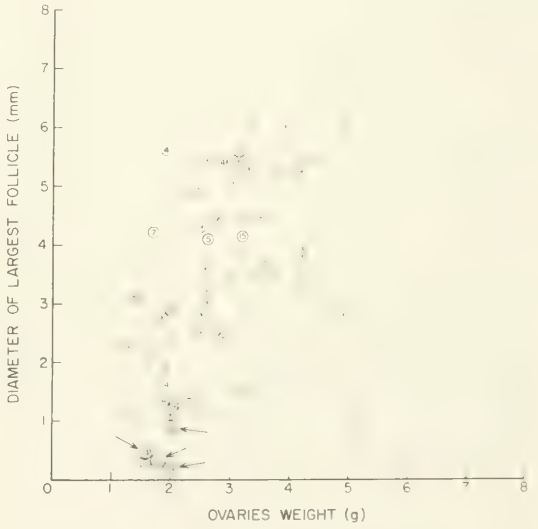

FIGURE 28.—Scatterplot of diameter of largest follicle on combined weight of ovaries for 73 adult female eastern spinner dolphins classified as "resting" (not pregnant or lactating). Specimens with corpora lutea or cystic follicles not included. Number in circle is total number of corpora in ovaries (including corpus luteum). Double circles are specimens with no Types 1 or 2 corpora albicantia indicating recent ovarian activity. Four postreproductive females indicated with arrows.

females truly resting, i.e., not ovulating because of being between cycles, those which have just ovulated but did not get pregnant, some with extremely small embryos missed in dissections, those which have recently aborted, and those which have prematurely terminated lactation due to death of the suckling calf.

The gestation phase of the cycle was estimated above, at 10.6 mo. We estimated average length of lactation by two methods; 1) by assuming that the proportion of a sample of mature females in a particular reproductive phase is directly proportional to the relative length of that phase in the overall cycle, i.e., that the samples are not biased with regard to reproductive phase (the length of the "resting" phase was also estimated this way); and 2) by assuming that a suckling calf exists for each lactating female, and the samples are unbiased with respect to suckling calves and lactating females, under which assumptions the length at which the cumulative frequency of calves in a sample equals the number of lactating females should be the average length (and, from the growth equation, age) at weaning. The first estimate was based on data for 536 adult females collected 1971–75, classified as pregnant, lactating, pregnant and lactating, "resting," or postreproductive (Table 7). The resting females were further subdivided into those with and without a corpus luteum. As discussed above, some proportion of those with a corpus luteum can be assumed to represent females not truly resting (with a corpus luteum of infertile ovulation). Only three females were simultaneously pregnant and lactating (1.44% of lactating females).

Subtraction of the postreproductive females and allocation of the females both pregnant and lactating to both of the two categories provides estimates of the proportions of the reproductive females in the three phases of the cycle (Figure 29) and of the relative lengths of the phases. Estimated average length of the phases and the total cycle can then be calculated for each 1-yr sample and for the pooled samples, using the estimated gestation

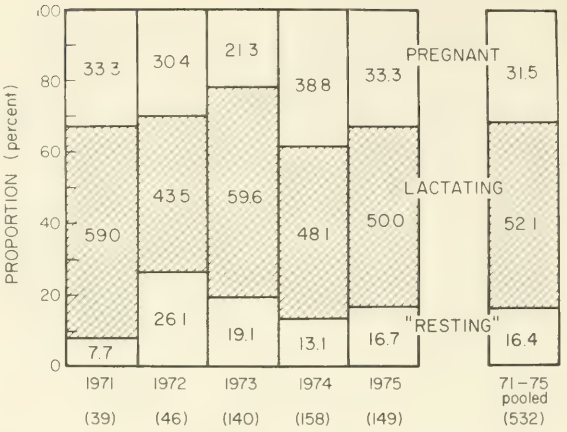

FIGURE 29.—Proportions of 532 adult reproductive female eastern spinner dolphins in pregnant, lactating, and "resting" (not pregnant or lactating) phases of cycle. Based on Table 4. Females both lactating and pregnant alloted to both phases. Postreproductive females excluded.

period of 10.6 mo (Method 1 in Table 8). The estimates of average length of lactation thus derived range from 13.1 to 29.7 mo (the possible causes of this wide year-to-year variation in phase structure of the samples are discussed below in Gross Annual Reproduction), with a pooled average of 17.5 mo.

The second method of estimating length of lactation, the "cumulative calf length/lactating females" method yielded estimates for six single-month samples ranging from 7.7 to 16.0 mo and for single-year samples from 9.4 59 10.6 mo (Method 2 in Table 8). The pooled estimate for 1973-75 is 10.1 mo. The three yearly estimates are consistent with each other and sharply lower than the estimates yielded by the "proportion-in-phase" method above (compare in Table 9). The first method could be invalid and cause disparate estimates if 1) lactating females (and their nursing calves) were overrepresented in the samples, or conversely, 2) either (or both) pregnant or "resting" females were underrepresented. This situation could obtain if lactating females and their

TABLE 7.—Reproductive condition of 536 adult female eastern spinner dolphins collected 1971-75.

	1971		1972		1973		1974		1975		1971-75 pooled	
Condition	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Pregnant only	13	33.3	14	30.4	29	20.6	60	37.3	49	32.9	165	30.8
Lactating only	23	59.0	20	43.5	83	58.9	75	46.6	74	49.7	275	51.3
Pregnant and lactating	0	0	0	0	1	0.7	2	1.2	1	0.7	4	0.7
"Resting"												
with corpus luteum	0	0	4	8.7	3	2.1	5	3.1	3	2.0	15	2.8
without corpus luteum	3	7.7	8	17.4	24	17.0	16	9.9	22	14.8	73	13.6
Postreproductive	0	0	0	0	1	0.7	3	1.9	0	0	4	0.7
Total	39	100.0	46	100.0	141	100.0	161	100.0	149	100.0	536	100.0

TABLE 8.—Estimated lengths of postreproductive phases, under two methods of estimating length of lactation, of the eastern spinner dolphin based on single-year samples, 1971-75, and on pooled samples for all years, with estimates of pregnancy rate and calving interval based on lactation estimate 1.

Item	1971	1972	1973	1974	1975	Pooled
Sample size (no.)	39	46	140	158	149	532
Pregnancy (months)	10.6	10.6	10.6	10.6	10.6	10.6
Lactation (months):						
Method 1	18.8	15.2	29.7	13.1	15.9	17.5
Method 2						
(Hyp. II)	—	—	10.6	9.4	10.2	10.1 (1973-75)
"Resting" (Method 1)	2.6	9.1	9.5	3.6	5.3	5.5
Sum of phases:						
Method 1						
(months)	32.0	34.9	49.8	27.4	31.8	33.6
(years)	2.66	2.91	4.15	2.28	2.65	2.80
Method 2						
(months)	—	—	26.7	25.5	26.3	26.2
(years)	—	—	2.23	2.13	2.19	2.18
Annual pregnancy rate (APR):						
Method 1	0.375	0.344	0.243	0.444	0.380	0.360
Method 2	—	—	0.450	0.474	0.459	0.461
Calving interval (1/APR):						
Method 1						
(years)	2.66	2.91	4.12	2.25	2.63	2.78
(months)	32.0	34.9	49.5	27.0	31.6	33.4
Method 2						
(years)	—	—	2.22	2.11	2.18	2.17
(months)	—	—	26.6	25.3	26.2	26.1

TABLE 9.—Estimates of length of lactation in the eastern spinner dolphin based on the "cumulative calf length/lactating females" method (see text), for 6 single-month samples and for 1973-75 by year and pooled.

Sample	Lactating females[1] (no.)	Length at which cumulative number of calves = number of lactating females (cm)	Length of lactation (months, under Hypotheses)		
			Layers	I	II and III
Feb. 1973	41	139	1.83	14.6	16.0
Mar. 1973	18	133	1.52	12.2	12.2
Jan. 1974	23	124	1.16	9.3	9.3
Feb. 1974	42	118	0.97	7.7	7.7
Jan. 1975	33	132	1.48	9.4	9.4
Feb. 1975	12	120	1.03	8.2	8.2
Year:					
1973	91	128.5	1.33	10.6	10.6
1974	81	124.5	1.18	9.4	9.4
1975	88	127.0	1.27	10.2	10.2
Pooled	260	126.7	1.26	10.1	10.1

[1] Includes mature females (≥165 cm) without lactation data prorated to lactating and nonlactating based on proportions in sample with lactation data.

accompanying calves are more likely to be captured and killed in the net because of limitations imposed on endurance of the mother by that of the calf, certainly lower than adult endurance. The second method could yield erroneous estimates if 1) nursing calves were overrepresented in the samples, or, conversely, 2) lactating females were underrepresented. Recent data for *S. attenuata* (J. E. Powers pers. commun.) indicate that small calves are probably overrepresented in small single-set samples of that species. This may be caused by the above-mentioned lesser stamina of calves in the energetically stressful purse seine chase, capture, and release sequence. The lesser year-to-year variation in the estimates yielded by Method 2 also supports the idea that these may be better estimates. If neonates are overrepresented in the samples, however, then the percent pregnant must be underestimated to some unknown, but small, degree. In view of these considerations, both the proportion-in-phase estimate and the cumulative calf length/lactating female estimate are used below as alternatives in estimating pregnancy rate, calving interval, and gross annual reproduction, and we conclude that the true length of lactation in an unperturbed birth-to-weaning period can be assumed to lie somewhere between the estimates yielded by the two methods.

Annual pregnancy rate by Method 1 was calculated by division of the proportion pregnant (Figure 29) by the length of gestation (0.875 yr). The reciprocal of annual pregnancy rate is the esti-

mate of average calving interval. For the Method 2 estimates, calving interval was calculated by summing the phases, taking into consideration overlapping cycles by adjusting the effective length of lactation downward by a factor equal to the percentage of lactating females also pregnant. Lacking an independent estimate of the length of the "resting" phase, the Method 1 estimate for 1973-75 was used as a reasonable approximation in the Method 2 calculations of length of cycle and calving interval.

CHANGES IN REPRODUCTIVE RATES WITH AGE.—Pregnancy rate in the sample decreases with age after about 12 layers (8.0, 11.5, or 10.2 yr, depending upon whether layer Hypothesis I, II, or III is applied, respectively), while lactation rate rises (Figure 30). Assuming that the samples are representative of the population, this may mean that 1) pregnancy rate decreases with age in the individual, or 2) that older females belong to older cohorts in which reproductive rates have been lower than in younger cohorts since recruitment to the breeding population. The former seems most likely; it would appear that older females have fewer calves and nurse them longer. The same result was obtained for *S. attenuata* in the eastern Pacific (Perrin et al. 1976).

Sex Ratios

Sex ratios are at or very near parity at birth and overall in the samples (Table 10), but there were slightly more females than males in adults in the samples for each of the 3 yr 1973–75, a result consistent with that encountered in *S. attenuata* (Perrin et al. 1976) but less pronounced.

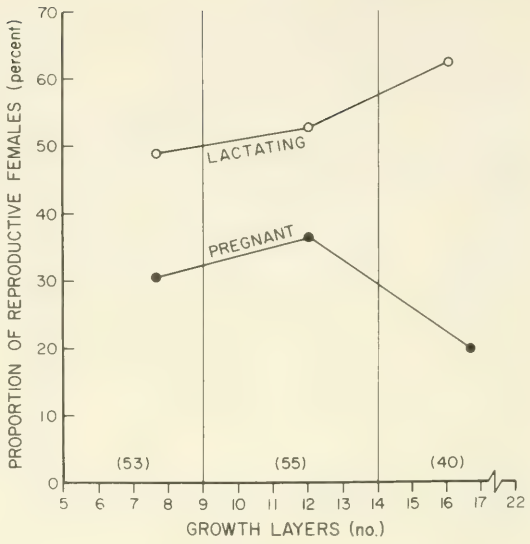

FIGURE 30.—Change in reproductive rates with age in the eastern spinner dolphin. Sample sizes in parentheses.

Gross Annual Reproduction

Estimates of gross annual reproductive rates can be made based on 1973–75 samples, the 3 yr for which the samples are large and nonselected with respect to age and sex structures (Table 11). It must be noted that if, as discussed above, small calves are overrepresented in small samples (which make up most of the aggregate sample), then the proportion of total females which are reproductive and pregnancy rate (for Method 1) are underestimated and the proportion of total sample female is overestimated, all to an unknown, but probably small, degree. Standard er-

TABLE 10.—Sex ratios in 126 fetuses and 2,261 neonatal-to-adult eastern spinner dolphins. Fetal samples limited to fetuses longer than 15 cm.

Stage	Length (cm)	Sample size (no.)	Average length (cm)	Females		Males		Sex ratio (M ÷ F)
				No.	%	No.	%	
Fetuses	>15	126	49.0	65	51.6	61	48.4	0.94
Neonates to adults	70-129	294	116.0	140	47.6	154	52.4	1.10
	130-149	269	141.2	132	49.1	137	50.9	1.04
	150-159	362	154.9	186	51.4	176	48.6	0.95
	·160 (adult size):							
	1973	408	171.2	207	50.7	201	49.3	0.97
	1974	439	171.3	226	51.5	213	48.5	0.94
	1975	483	172.4	254	52.6	229	47.4	0.90
	1973-75 pooled	1,330	171.7	687	51.7	643	48.3	0.94
	Total:[1]							
	1973	688	—	342	49.7	346	50.3	1.01
	1974	797	—	395	49.6	402	50.4	1.02
	1975	776	—	411	53.0	365	47.0	0.89
	1973-75 pooled	2,261	—	1,148	50.8	1,113	49.2	0.97

[1]Includes six specimens for which length data not available.

TABLE 11.—Calculation of estimates of gross annual reproductive rate of the eastern spinner dolphin, 1973-75. Standard error follows estimate (see text). Sample sizes in parentheses.

Year	*A* Proportion female	*B* Proportion of females reproductive	*C* Annual pregnancy rate		*A* × *B* × *C* Gross annual reproductive rate	
			Method 1	Method 2	Method 1	Method 2
1973	0.497 ±0.019 (690)	0.443 ±0.027 (343)	0.243 ±0.036 (140)	0.450 ±0.042 (140)	0.054 ±0.009 (690)	0.099 ±0.011 (690)
1974	0.496 ±0.018 (797)	0.438 ±0.025 (391)	0.444 ±0.040 (158)	0.474 ±0.042 (158)	0.096 ±0.010 (797)	0.103 ±0.011 (797)
1975	0.530 ±0.018 (776)	0.432 ±0.024 (410)	0.380 ±0.040 (149)	0.459 ±0.041 (149)	0.087 ±0.010 (776)	0.105 ±0.011 (776)
1973-75 pooled	0.508 ±0.011 (2,262)	0.437 ±0.015 (1,144)	0.360 ±0.028 (447)	0.461 ±0.024 (447)	0.080 ±0.006 (2,262)	0.102 ±0.006 (2,262)

rors (SE) are attached to the various estimates where sample size ⩾100, under the assumption that the binomial distribution tends to normality in large samples (Bailey 1959), allowing calculation of SE as:

$$SE = \sqrt{p(1-p)/n}.$$

Although gross annual reproductive rate as calculated in Table 11 is a product of three estimates, it can be calculated directly from the total sample (number of females pregnant ÷ total number of males and females), allowing estimation of the variance by the above method. The effect on the variance by the constant used to adjust the pregnancy rate to an annual rate was ignored because the constant (11.5 mo gestation ÷ 12 mo, or 0.958) is close to unity.

The only statistically significant differences among the estimates year-to-year (at $\alpha = 0.05$) are between the Method 1 estimates for 1973 and 1974 of annual pregnancy rate and, as a result of that, gross annual reproductive rate. This sharp and real shift cannot be accounted for by a time-sampling effect, because seasonal coverage in the 2 yr was approximately the same. Prompted by the knowledge that areal variation may exist in the timing of calving peaks and/or in the degree of breeding synchrony (see Length of Gestation and Fetal Growth), we divided the data for each of the years into three geographical strata: an "inside" sample, an "outside" sample, and a "southern sample" (Figure 31). More of the 1973 sample was taken from the outside area than from the inside area (108 versus 28), and the reverse was true in 1974 (46 versus 106). The southern samples, 5 in 1973 and 14 in 1974, were too small for analysis. Comparison of the distribution of reproductive condition in inside and outside samples in 1973 and 1974, however, reveals very small areal differences compared with those between years (Table 12). It must be concluded that the sharp increase in percent pregnant and decrease in percent lactating from 1973 to 1974 is not a seasonal or areal effect. Several other possible explanations exist, to wit:

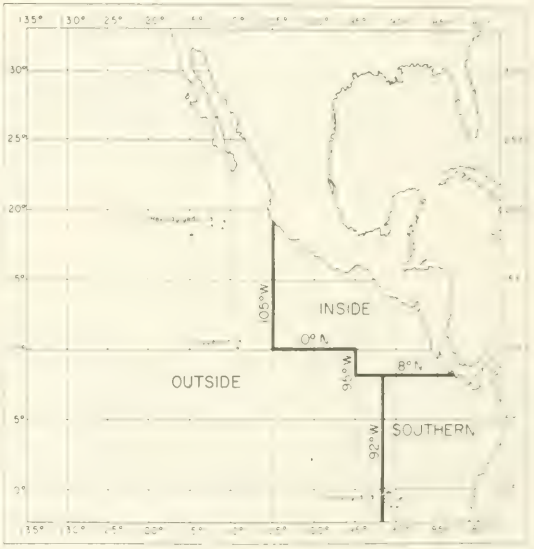

FIGURE 31.—Areas used to stratify 1973-74 samples of distribution of reproductive condition in female eastern spinner dolphins.

TABLE 12.—Distribution of reproductive condition in area-stratified samples of sexually adult female eastern spinner dolphins in 1973 and 1974.

Year	Inside (n = 134)	Outside (n = 154)
	(n = 28)	(n = 108)
1973	14.3% pregnant	19.4% pregnant
	57.1% lactating	61.1% lactating
(n = 136)	3.6% pregnant and lactating	0.0% pregnant and lactating
	25.0% "resting"	18.5% "resting"
	0.0% postreproductive	0.9% postreproductive
	(n = 106)	(n = 46)
1974	38.7% pregnant	39.1% pregnant
	48.1% lactating	50.0% lactating
(n = 152)	0.0% pregnant and lactating	4.3% pregnant and lactating
	10.4% resting	6.5% resting
	2.8% postreproductive	0.0% postreproductive

1) The samples were biased with respect to reproductive structure of the population, in one or both years or differently in the 2 yr.
2) The change was a real and normal event, perhaps reflecting differential breeding rates in single-year cohorts (the data suggest about a 3-yr cycle—see below—and the 1974 rates were similar to those for 1971).
3) An anomalous increase in pregnancy rate occurred from 1973 to 1974, perhaps related to exploitation in the tuna fishery or to natural variation in the pelagic environment.

The balance of evidence discussed above favors the first alternative, suggesting that the Method 2 estimates of gross annual reproduction are the more accurate of the two alternative sets of estimates.

DISCUSSION

Comparison with the Spotted Dolphin

The estimated gross reproductive rates (Method 1) for the eastern spinner dolphin are lower than those estimated for the offshore spotted dolphin by Perrin et al. (1976), 10 to 11%, as opposed to 14%. Three major points of difference between the data for the two species contribute to this disparity.

1) A higher proportion of the spotted dolphins were females (55.1% as opposed to 50.8% in the present 1973–75 sample of eastern spinner dolphins).
2) The proportion of total females which were reproductive was higher for the spotted dolphin (55.7% as opposed to 43.7% for the eastern spinner dolphin).
3) There is apparently much less overlapping of reproductive cycles in the eastern spinner dolphin than in the spotted dolphin in the eastern Pacific. Only 1.4% of lactating females examined were simultaneously pregnant, as opposed to 9.6% in the spotted dolphin, a sevenfold difference. At least part of this difference may be inherent in the species; the rate in the unexploited western Pacific population of spotted dolphin is 5.1% (Kasuya et al. 1974), still nearly four times greater than in the eastern spinner dolphin.

In summary, the data suggest that there is an inherent difference in reproductive capability between the spotted and spinner dolphins, but that part of the total difference in present reproductive rate may be related to differential exploitation. Gross annual reproductive rate in the unexploited western Pacific population of *S. attenuata* is estimated at 0.094 (calculated from data in Kasuya et al. 1974—0.57 female × 0.61 mature × 0.27 annual pregnancy rate = 0.094/yr), as opposed to 0.144 in the exploited eastern Pacific population of the same species, a possible example of difference in rate correlated with differential exploitation. Whereas the western Pacific population is thought to be virtually unexploited and at its original size, the eastern Pacific population is estimated to be at 62% of its original, preexploitation size (midpoint estimate).[8]

Comparison with Other Cetaceans

The estimates of gross annual reproductive rate for the eastern spinner dolphin lie at the lower end

[8]Report of the Workshop on Stock Assessment of Porpoises Involved in the Eastern Pacific Yellowfin Tuna Fishery. SWFC Admin. Rep. LJ-76-29, Natl. Mar. Fish. Serv., NOAA, La Jolla, Calif., 109 p. (Unpubl. rep.)

TABLE 13.—Estimated gross annual reproductive rate of the eastern spinner dolphin compared with estimated rates for other cetaceans. Data for *S. attenuata* from Perrin et al. (1976) for eastern Pacific and Kasuya et al. (1974) for western Pacific; for *S. coeruleoalba* from Kasuya (1972), for *Delphinus* from Danilevskiy and Tyutyunnikov (1968); for *Globicephala* from Sergeant (1962); for *Delphinapterus* from Sergeant (1973); and for *Eschrichtius* from Rice and Wolman (1971). Common and scientific names follow Subcommittee on Small Cetaceans, Scientific Committee, IWC (Anonymous 1975); alternative common name in parentheses.

Species and locality	Exploited (now or in past)	Gross annual reproductive rate
Eastern spinner dolphin (porpoise), *Stenella longirostris* subsp.	Yes	0.08 (pooled 1973-75)
Spotted dolphin (porpoise), *S. attenuata*		
Eastern Pacific	Yes	0.14
Western Pacific	No	0.09
Striped dolphin (streaker porpoise), *S. coeruleoalba*, in western Pacific	Yes	0.11
Common dolphin (whitebelly porpoise), *Delphinus delphis*, in Black Sea	Yes	0.14
Long-finned pilot whale (pothead whale), *Globicephala melaena*, in western North Atlantic	Yes	0.10 to 0.13
White whale (beluga), *Delphinapterus leucas*, in western Hudson Bay	Yes	0.12
Gray whale, *Eschrichtius robustus*, in eastern North Pacific	Yes	0.13

of the range of estimates for other cetaceans (Table 13), with only the estimate for 1974 included in the range. The estimated rates for populations thought to have declined due to exploitation (*S. attenuata* in the eastern Pacific—Perrin et al. 1976; *D. delphis* in the Black Sea—Danilevskiy and Tyutyunnikov 1968; and *Eschrichtius*—Rice and Wolman 1971) are very close to each other, at 13 or 14%.

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PRODUCTION BY THREE POPULATIONS OF WILD BROOK TROUT WITH EMPHASIS ON INFLUENCE OF RECRUITMENT RATES

ROBERT F. CARLINE[1]

ABSTRACT

Populations of wild brook trout, *Salvelinus fontinalis,* in three small ponds in northern Wisconsin were studied for 4 yr to determine annual production with particular emphasis on influence of recruitment rates. Recruitment included trout hatched in ponds and immigrants from adjacent waters. Age-specific growth rates and densities of trout were estimated in spring and fall. Harvest of trout was estimated through partial creel surveys.

Among populations annual production ranged from 26 to 331 kg/ha and was directly related to recruitment rates. Production was most influenced by population biomass. Instantaneous growth rates did not vary significantly within or among populations despite large differences in population densities; hence, variations in production appeared unrelated to growth rates. Among populations, yield of trout ranged from 25 to 72 kg/ha and fishing pressure ranged from 154 to 1,405 h/ha. Proportion of annual production that was harvested was directly related to fishing pressure.

Production of fry during the first 9 mo of life may have been overestimated because mortality rates from emergence to fall were assumed constant. Estimates of production of adult trout could have been positively or negatively biased depending upon immigration patterns. Despite these possible errors, it was clear that recruitment was the most important factor affecting production.

Estimation of fish production has gained widespread acceptance because it provides some measure of a system's capacity to support species of interest (Gerking 1967). Production is defined as the total elaboration of tissue by a population during a specified time interval, regardless of the fate of that tissue (Ivlev 1945). Unlike standing crop estimates, production is a dynamic population parameter that is useful in evaluating the environmental performance of a fish population (Le Cren 1972). Studies by Ricker and Foerster (1948), Allen (1951), and Hunt (1971) are good examples of how fish production has been related to predation, the food supply, and habitat suitability. While many studies have considered the effects of standing crops, growth rates, and mortality on production, the importance of recruitment has not been well defined.

In northern Wisconsin, standing crops of wild brook trout, *Salvelinus fontinalis,* in spring-fed ponds vary greatly. Some ponds have filled-in naturally and living space is limiting. In others, living space appears to be adequate, but spawning areas are small or nonexistent and recruitment seems to be limiting standing crops of trout. The objective of this study was to determine annual production by three populations of wild brook trout with particular emphasis on the influence of recruitment rates. Recruitment includes all trout hatched in the ponds plus all immigrant trout.

The ponds were chosen because they differed greatly in areas available for spawning and numbers of immigrating trout. Ponds were similar in size and watershed characteristics, and springs were the primary sources of water. Outlet streams, which flowed into larger streams and/or lakes, provided convenient sampling boundaries, but did not impede movement of trout into or out of the ponds. I estimated densities and growth rates of trout every spring and fall from 1968-72 and conducted partial creel surveys during 3 yr of the study to estimate trout yields.

DESCRIPTION OF STUDY AREA

The study ponds, situated in a terminal moraine, are located within 7 km of each other in Langlade County, north central Wisconsin. The moraine is composed of glacial till ranging in size from sand to large boulders. These permeable

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materials permit a relatively uninhibited flow of ground water that is the main source of water for all ponds. Hoglot and Clubhouse springs are on state-owned land and Maxwell Springs is privately owned. The ponds are located in wooded lowlands and all three drain into trout streams that are part of the Wolf River drainage, a major Lake Michigan watershed.

The ponds are similar in size and have relatively short exchange times due to large inflows of ground water (Table 1). Because all ponds are supplied by the same aquifer, concentrations of common ions are similar. Bottom materials consist mostly of marl and organic matter. About 10% of the shorelines in Maxwell and Hoglot springs are composed of gravel with emerging ground water and brook trout spawn in these areas. Numbers of trout redds in Hoglot Springs ranged from 85 to 105/ha of pond area, and in Maxwell Springs redd densities ranged from 165 to 230/ha. Clubhouse Springs lacks gravel areas with upwelling ground water and brook trout do not spawn there.

Continual inflow of ground water and rapid exchange times tend to moderate pond temperatures and maintain relatively high concentrations of dissolved oxygen. Ground water temperatures typically range from 6° to 7°C and concentrations of dissolved oxygen, from 8 to 9 ppm. Pond temperatures in summer at depths of 15 cm rarely exceed 16°C. Concentrations of dissolved oxygen rarely fall below 5 ppm at any depth throughout the year and they usually exceed 7 ppm. Ponds are ice-covered from early November to late March.

All ponds supported dense beds of aquatic vegetation. *Chara vulgaris* covered about 40% of the bottom in Clubhouse Springs and 15% in Hoglot Springs. *Anacharis canadensis,* the only common plant in Maxwell Springs, extended over 50% of the bottom.

TABLE 1.—Some physicochemical features of study ponds in north central Wisconsin. Chemical measurements were taken in April 1970.

Item	Clubhouse Springs	Hoglot Springs	Maxwell Springs
Surface area (ha)	0.81	0.38	0.97
Mean depth (m)	1.11	0.64	0.86
Outlet discharge[1] (m^3/s)	0.03	0.005	0.05
Exchange time[2] (days)	3.3	5.6	2.0
Specific conductance (μmho/cm)	341	335	310
Total alkalinity (mg/l as $CaCO_3$)	180	153	168
Calcium (mg/l)	42	40	39
Nitrate (mg/l-N)	0.5	0.7	1.1
Dissolved phosphorus (mg/l-P)	0.02	0.01	0.03

[1]Summer base flow.
[2]Pond volume/discharge.

Fish communities in the three ponds were similar. Brook trout composed the major portion of fish biomass. A small population of brown trout, *Salmo trutta,* in Clubhouse Springs never accounted for more than 10% of the total number of trout. The white sucker, *Catostomus commersoni*; mottled sculpin, *Cottus bairdi*; Central mudminnow, *Umbra limi*; and brook stickleback, *Culaea inconstans*, were common in all ponds. The brook stickleback was an important food source for age 3 and older trout; however, benthic invertebrates composed the major portion of the diet for trout of all sizes.

METHODS

Trout populations were estimated in spring and fall using Bailey's modification of the Petersen mark and recapture method (Ricker 1975). Trout were captured at night with electrofishing gear and held overnight in screen cages. The following day, fish were anesthetized, measured to the nearest 2 mm (total length), weighed to the nearest gram, given a temporary mark by clipping the tip of the caudal fin, and released. A second electrofishing run was made two or more days later. Proportions of marked trout captured during the second electrofishing sample were used to calculate confidence limits for population estimates (Adams 1951).

Age structures of trout populations were determined from length distributions of known age fish and scale analyses. Fall fingerlings and spring yearlings, determined from length-frequency distributions, were permanently marked by fin removal. Estimated numbers of trout in each 25-mm length group were placed in appropriate age-groups based on relative proportions of known age fish. The electrofishing gear was size selective. Efficiency was lowest for smallest fish and increased until fish size reached about 12 cm. Separate estimates for 25-mm length intervals avoided bias due to size selectivity of electrofishing gear.

Maxwell outlet and Elton Creek, the stream into which Clubhouse Springs flowed, were sampled with electrofishing gear to obtain data on growth rates of trout in outlet waters and on movement of trout between ponds and adjoining streams. A 1-km section of Elton Creek was sampled five times from 1968 to 1971; Clubhouse

outlet joined this section at its midpoint. Maxwell outlet (200 m) was sampled in 1969 and 1972. All trout were measured, about 25% were weighed, and fall fingerlings and spring yearlings were permanently marked by fin removal.

Sampling dates in ponds varied from year to year. I estimated mean lengths and weights of each cohort on 15 April and 15 September so that growth rates from different years could be compared. Mean weights of individuals in each year class were determined graphically by assuming constant instantaneous rates of growth. By graphically estimating mean length, I assumed length increased linearly between successive estimates. Most of the adjustments in length or weight involved extrapolating over periods <2 wk and size changes were usually <5%.

Year class biomass was estimated by multiplying mean weights of individual trout by year class density. Biomasses in spring and fall were averaged to calculate mean biomass ($\bar{B}$). I followed procedures suggested by Ricker (1975) to calculate instantaneous rates of growth by weight (G), total mortality (Z), natural mortality (M), and fishing mortality (F). Production, the product of G and $\bar{B}$, was computed semiannually for each cohort. Production by fingerling trout was calculated from emergence (1 March) to time of spring population estimate and from spring to fall. A mean weight of 0.04 g was assigned to emergent fry (Hunt 1966). I assumed that instantaneous growth and mortality rates from emergence to fall were constant. Mean annual biomass of each cohort was calculated by weighting mean biomasses in the two intervals according to interval lengths. Annual production was calculated by summing production during the two intervals and expressing the sum for 365-day periods.

Potential egg production for each population was estimated from numbers of mature females in fall and from a relationship between total length of females and number of eggs. Fecundity of trout was determined from 83 females that were collected from two ponds in the same watershed as the study ponds. Trout were collected in early October, about 2 wk prior to spawning. Mature ova could be easily distinguished from recruitment eggs on the basis of size and color (Vladykov 1956). Data on trout length, weight, and total number of eggs were fitted to linear, curvilinear, and logarithmic regression models. A linear regression of total trout length and number of eggs yielded the highest correlation coefficient.

At Clubhouse and Hoglot springs, densities of some year classes increased during sampling intervals because of immigration from outlets or adjoining streams. Numbers of immigrants were estimated by first calculating expected densities at the end of sampling intervals by using mean, age-specific mortality rates; expected densities were then subtracted from actual densities. If the expected number of trout at the end of an interval was within 10% of the actual number or the difference was negative (suggesting emigration), it was assumed no immigration had occurred. Age-specific mortality rates for trout in Clubhouse and Hoglot springs were estimated from permanently marked fish. For some age groups, mortality rates could not be estimated because of insufficient numbers of marked fish. In these instances I used age-specific mortality rates of the population in Maxwell Springs, where immigration did not influence year class densities (discussed later).

Harvest of trout from Clubhouse and Hoglot springs was estimated from partial creel surveys in 1969, 1970, and 1972. State-wide angling regulations included a bag limit of 10 trout/day and minimum length of 154 mm (6 in). Census clerks worked five randomly.chosen days per week during the entire fishing season, mid-May to mid-September. Catch rates were estimated from data collected during interviews of anglers, and fishing pressure was calculated from instantaneous counts of anglers (Lambou 1961). Harvest was estimated monthly from the product of the hours of fishing and numbers of trout caught per hour. Harvested trout were measured, examined for permanent marks, and scales were collected from a sample of the catch. Harvest data from Maxwell Springs were compiled by the owner and others who fished the pond. Ages of harvested trout from Clubhouse and Hoglot springs were determined from scales and size distributions of permanently marked fish. Ages of trout harvested from Maxwell Springs were estimated from comparisons of lengths of harvested trout with lengths of known age fish in spring and fall.

RESULTS

Population Densities and Biomass

Electrofishing was the most efficient method of collecting trout in these shallow ponds. Population estimates derived from collections with trap

nets and seines showed that collecting trout with just electrofishing gear did not yield biased estimates (Carline unpubl. data). Efficiency of the electrofishing gear usually increased with trout size (Table 2). Mean proportions of marked trout captured during the second electrofishing sample for age 0 to 3 fish were 0.18, 0.31, 0.35, and 0.39, respectively. Recapture efficiencies were always lowest for age 0 trout and values ranged from 0.05 to 0.30. For age 1 and older fish, precision of estimates depended mostly upon sample size and confidence limits for the oldest age groups were generally broad because of their low densities (Table 2).

TABLE 2.—Examples of trout population estimates and 95% confidence limits by age-groups. Data were collected in fall 1970.

Item	0	1	2	3	4
Clubhouse Springs:					
Mean length (mm)	99	175	211	274	
Proportion of marked fish recaptured	0.30	0.40	0.41	0.50	
Population estimate (no./ha)	386	363	84	6	
95% confidence limits	234	279	47	0	
	782	466	124	40	
Maxwell Springs:					
Mean length (mm)	92	147	182	220	287
Proportion of marked fish recaptured	0.05	0.43	0.53	0.34	0.22
Population estimate (no./ha)	2,195	1,572	909	433	28
95% confidence limits	1,183	1,408	845	367	17
	3,944	1,778	1,003	507	56

Clubhouse Springs

The brook trout population in Clubhouse Springs was the smallest of the three populations. Because no spawning areas were present, this population was entirely dependent upon immigration from downstream areas. Trout densities usually declined from spring to fall and only age 0 trout appeared to immigrate in substantial numbers oversummer (Figure 1). Total trout numbers in 3 of 4 yr increased overwinter due to immigration. Numbers of trout in spring ranged from 390 to 1,750/ha and densities in fall ranged from 390 to 840/ha. Age structure of the population was at times atypical because young age groups were less numerous than older ones, owing to differential rates of immigration.

Changes in population biomass closely paralleled numerical changes. Biomass in spring averaged 45 kg/ha and in fall 26 kg/ha (Table 3). In all years, population biomass increased from fall to spring, the period when immigration appeared greatest.

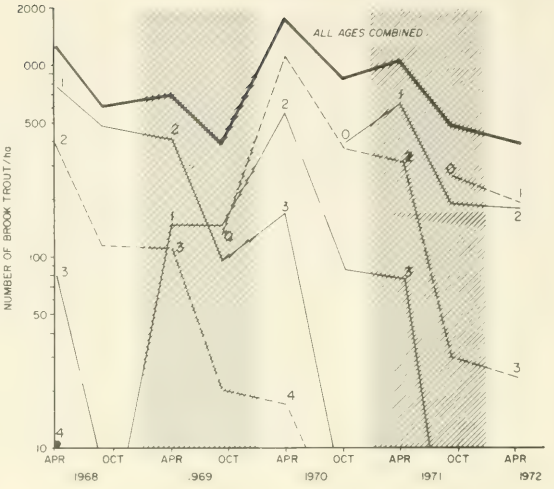

FIGURE 1.—Estimated numbers of brook trout in Clubhouse Springs, 1968-72. Numbers designate age-groups and hatched areas separate calendar years.

TABLE 3.—Estimated biomass (kilograms per hectare) by age-group of brook trout in study ponds, 1968-72. Mean weights of individuals in each age-group were multiplied by estimated density of the age-group to calculate biomass.

Site and date	0	1	2	3	4	5	Total
Clubhouse Springs:							
27 Mar. 1968		10.9	15.6	8.7	3.5		38.7
28 Aug. 1968		22.9	10.8	1.2	1.7		36.6
8 Apr. 1969		3.0	23.7	14.4	5.2		46.3
8 Sept. 1969	1.8	7.6	10.4	4.3	0.4		24.5
1 Apr. 1970		17.2	26.2	20.4	4.6		68.4
8 Sept. 1970	3.5	17.4	7.0	1.2			29.1
29 Apr. 1971		12.0	22.9	12.2	2.3		49.4
8 Sept. 1971	2.1	6.6	3.1	0.2			12.0
21 Apr. 1972		3.0	13.1	4.4	0.7		21.2
Hoglot Springs:							
2 Apr. 1968		22.6	69.1	26.5	11.2		129.4
26 Aug. 1968	6.8	26.1	35.8	13.6	3.6		85.9
8 Apr. 1969		5.0	37.2	66.8	8.1		117.1
8 Sept. 1969	15.9	33.7	47.6	12.5	2.3		112.0
13 Apr. 1970		13.0	38.3	38.5	13.3		103.1
8 Oct. 1970	16.9	91.0	36.4	9.1	0.7		154.1
28 Apr. 1971		10.8	70.7	21.5	2.1		105.1
21 Sept. 1971	7.0	26.6	40.7	5.6	0.2		80.1
2 May 1972		10.8	17.0	6.5	2.5		36.8
Maxwell Springs:							
9 Apr. 1969		34.4	50.8	26.3	41.6	80.3	233.4
13 Oct. 1969	27.0	55.8	88.8	29.3	20.8	16.1	237.8
26 Mar. 1970		25.3	47.3	69.6	16.2	12.4	170.8
6 Oct. 1970	22.0	56.6	63.6	53.7	6.9	2.6	205.4
26 Apr. 1971		8.2	48.0	46.9	17.6	0.5	121.2
20 Sept. 1971	24.6	19.2	32.6	13.8	0.9		91.1
26 Apr. 1972		27.1	7.3	7.1	3.7		45.2
29 Sept. 1972	14.8	46.6	11.0	4.5	1.4		78.3

Hoglot Springs

Although some fingerlings were hatched in Hoglot Springs, numbers of immigrating trout, particularly age 1 fish, had the most impact on population size. In 3 of 4 yr, densities of yearling trout increased oversummer, and during the

winter of 1968-69 fall 2-yr-olds increased by 50% (Figure 2). Mean population densities were higher in fall than in spring (4,480 vs. 3,200/ha) because of recruitment by age 0 trout and age 1 trout.

Trout migrating into Hoglot Springs had a marked effect on population biomass. Biomass was highest in fall 1970 because of the large stock of yearlings (91 kg/ha), most of which were recent immigrants (Table 3). Little immigration occurred oversummer in 1971 and overwinter in 1971-72. As a result, population biomass in spring 1972 reached its lowest level of the 4-yr period.

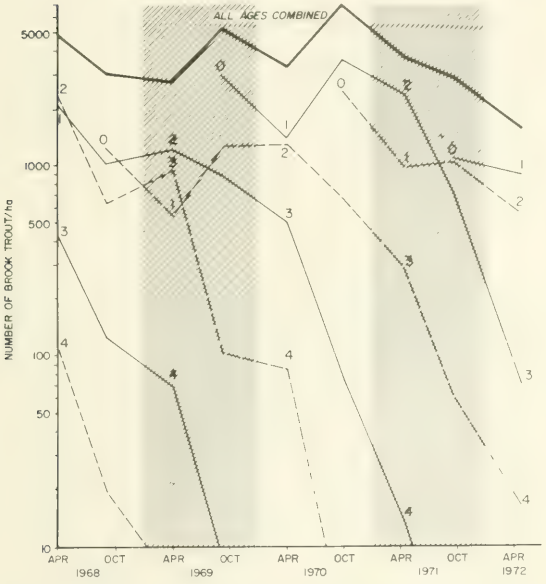

FIGURE 2.—Estimated numbers of brook trout in Hoglot Springs, 1968-72. Numbers designate age-groups and hatched areas separate calendar years.

Maxwell Springs

Except for 1972, Maxwell Springs supported the largest of the three populations, and natural reproduction accounted for nearly all recruitment. Two experiments were conducted to evaluate the extent of immigration from Maxwell outlet into the pond. In June 1969 and April 1972, a total of 602 ages 0 and 1 trout were captured in the outlet and marked. In subsequent surveys of the pond, I examined over 4,000 trout, only 3 of which had been marked in the outlet. Hence, I concluded that trout reared in the outlet did not materially affect recruitment in the pond.

From April 1969 to September 1972 trout densities in Maxwell Springs declined markedly (Figure 3). Spring densities steadily decreased from 7,300/ha in 1969 to 1,810/ha in 1972. Fall populations followed a similar trend. This decline was due in part to decreasing numbers of fall fingerlings. Densities of age 0 trout ranged from 4,085/ha in October 1969 to 1,940/ha in September 1972. However, even the 1969 year class, which was larger than the succeeding three year classes, had to be smaller than the 1968 and 1967 year classes, based on their densities as ages 1 and 2 fish in April 1969 (Figure 3). I estimated numbers of fall fingerling for the 1967 and 1968 year classes by using average mortality rates of succeeding year classes. The 1967 year class was estimated at 16,000/ha and the 1968 year class at 8,300/ha. Thus, numbers of fall fingerlings had steadily declined from 1967 to 1972 with one exception, the 1971 year class.

The reduction in year class strength in Maxwell Springs may have been related to the installation of a weir in the pond outlet in 1968. The weir, which was used to monitor discharge, was located 132 m downstream from the pond and it created

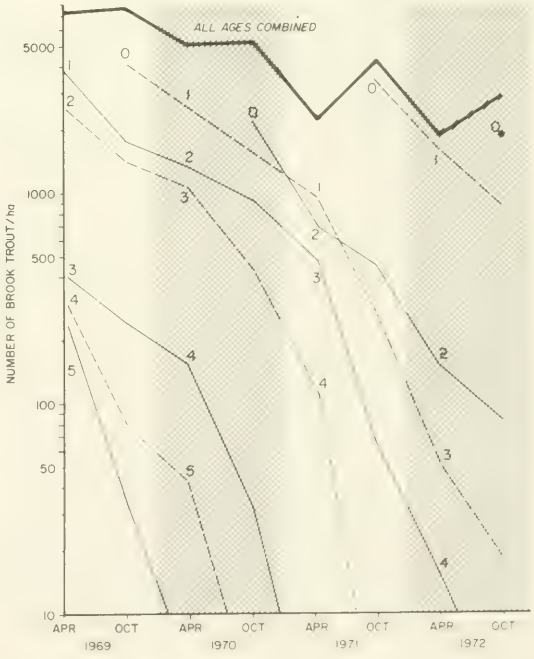

FIGURE 3.—Estimated numbers of brook trout in Maxwell Springs, 1969-72. Numbers designate age-groups and hatched areas separate calendar years.

an impoundment that extended to within 5 m of the pond. The impounded area was heavily silted by fall 1968 and I counted only four redds there. The owner had reported that large numbers of brook trout spawned in this area prior to weir installation. In fall 1974, 1 yr after the weir had been removed, I counted 34 redds and about half the streambed was covered with silt. Since effects of impoundment were still evident, this portion of the outlet may have provided much more spawning area than was evident in 1974. Possibly, immigration was an important source of recruitment prior to this study.

Population declines at Maxwell Springs were accompanied by changes in age structure. In April 1969, density of age 3 and older trout was nearly 1,000/ha and they totaled 233 kg/ha, or 63% of population biomass (Table 3). By September 1972, density of age 3 and older trout was 22/ha and biomass was about 6 kg/ha, the lowest in the 4-yr period.

Mortality

Numbers of fall fingerlings in Hoglot and Maxwell springs represented from 0.2 to 1% of the estimated number of eggs deposited the previous fall. I sampled 52 redds in five different ponds to assess preemergence mortality. Numbers of eggs per redd ranged from about 30 to 220. Percentage of live embryos in individual redds ranged from 76 to 99 (mean = 89%); stage of development of these embryos varied from eyed egg to alevin. Due to additional mortality to emergence, I used 80% of potential egg deposition to estimate numbers of emerging fry. Although highest mortality rates in both ponds occurred during years of highest egg production, egg production and fingerling mortality were not significantly correlated (Table 4).

To estimate age-specific total mortality rates of trout in Maxwell Springs, I assumed that immigration was negligible. At Clubhouse and Hoglot springs, where immigration was substantial, unmarked residents and immigrants could not be separated; therefore, mortality rates were calculated using only permanently marked trout. Numbers of age 2 and older trout were usually too small to allow estimation of mortality rates.

Mean rates of oversummer mortality in Maxwell and Hoglot springs increased with age (Table 5). Overwinter mortality rates at Maxwell Springs also increased with age, except that age 0 trout had higher mean mortality rates than did age 1 trout. However, within years there was considerable variability between age of fish and mortality rates. In all ponds mean mortality rates oversummer exceeded overwinter rates.

TABLE 4.—Estimated egg production of brook trout populations and densities of fall fingerlings. Egg deposition was estimated from number of mature female trout in fall and the relationship of fecundity (Y) and trout length in millimeters (X); $Y = -588 + 6.14X$. Instantaneous mortality rates (Z) were based on 80% of egg production and were corrected for 182-day intervals.

Pond	Year class	No. eggs/ha	No. fall fingerlings/ha	Z/182 days
Hoglot Springs	1969	281,000	2,938	4.111
	1970	276,000	2,481	3.681
	1971	433,000	1,049	5.148
	Mean	330,000	2,156	4.313
Maxwell Springs	1969	543,000	4,085	3.742
	1970	550,000	2,195	4.384
	1971	739,000	3,519	4.549
	1972	212,000	1,945	3.800
	Mean	511,000	2,936	4.119

Immigration

Estimation of immigration rates at Clubhouse and Hoglot springs were based on mortality rates calculated from relatively small numbers of permanently marked trout and from mean, age-specific mortality rates of trout from Maxwell Springs (Table 5). Although accuracy of these estimates is suspect, they should be useful in illustrating seasonal differences in immigration and in assessing the effect of immigration on recruitment.

At Clubhouse Springs most immigration occurred overwinter and age 0 trout made up 55% of all migrants (Table 6). Largest migrations into Hoglot Springs occurred between April and September when age 1 trout accounted for 73% of all migrants. In both populations periods of peak immigration coincided with highest population densities. Immigration was the only source of recruitment at Clubhouse Springs; at any one time more than half the population consisted of fish that had immigrated within the previous 6 mo. At Hoglot Springs percentages of recent immigrants ranged from 8.2 to 54.9 (mean = 34%).

If estimates of trout migrating into Hoglot Springs are reasonable, immigration accounted for a major portion of total recruitment. The four year classes produced in the pond from 1968 to 1971 amounted to 7,700 fall fingerlings/ha. About 3,800 of these fish survived to the following spring.

TABLE 5.—Instantaneous total mortality rates for 182-day intervals. Mortality rates of trout in Maxwell Springs were calculated from year class densities. Mortality rates of trout in Hoglot and Clubhouse springs were calculated from permanently marked fish. Estimated numbers of trout at the end of sampling intervals given in parentheses.

Interval and year	Maxwell Springs					Hoglot Springs		Clubhouse Springs
	[1]0	1	2	3	4	1	2	1
Oversummer:								
1968						2.254		1.238
						(72)		(75)
1969		0.766	0.573	0.510	1.521	0.408	2.151	1.914
		(1,691)	(1,368)	(233)	(109)	(110)	(7)	(13)
1970		0.448	0.373	0.850	1.492	0.725	1.080	1.489
		(1,525)	(882)	(420)	(31)	(158)	(8)	(81)
1971		0.500	1.552	2.439	4.404	1.382	1.631	1.522
		(442)	(264)	(62)	(3)	(33)	(20)	(65)
1972		0.681	0.670	1.185	1.532			
		(863)	(82)	(17)	(4)			
Mean		0.599	0.792	1.246	2.237	1.192	1.742	1.541
Overwinter:								
1968-69						0.175		0.804
						(58)		(28)
1969-70	0.530	0.282	0.306	0.826	1.085	1.312		1.662
	(2,457)	(1,310)	(1,039)	(110)	(41)	(23)		(2)
1970-71	1.048	0.444	0.606	1.243	2.498	0.687		0.573
	(664)	(931)	(450)	(106)	(2)	(74)		(39)
1971-72	0.659	0.917	1.398	1.211	0.926	0.826		1.186
	(1,549)	(147)	(49)	(14)	(1)	(12)		(15)
Mean	0.746	0.548	0.770	1.093	1.503	0.750		1.056

[1]Age at start of interval.

TABLE 6.—Estimated numbers of immigrant brook trout present by age-groups at the end of sampling intervals. Summer intervals were from April to September and winter intervals from September to the following April. Percent of population at the end of the interval composed of recently immigrated trout given in parentheses.

Year and interval	Clubhouse Springs					Hoglot Springs				
	0	1	2	3	Sum	0	1	2	3	Sum
1968										
Summer	0	346	0	0	346 (57)		207	42	0	249 (8)
Winter	147	277	65	14	503 (74)	0	802	659	34	1,495 (55)
1969										
Summer	130	104	0	0	234 (60)		1,046	619	0	1,665 (32)
Winter	955	514	130	12	1,611 (92)	191	767	149	56	1,163 (36)
1970										
Summer	387	102	0	0	489 (58)		3,205	417	0	3,622 (53)
Winter	451	215	46	6	718 (70)	0	773	0	0	773 (21)
1971										
Summer	262	0	0	0	262 (55)		645	133	0	778 (27)
Winter	86	128	12	0	226 (57)	478	157	0	0	635 (41)
Sum	2,418	1,686	253	32	4,389	669	7,602	2,019	90	10,380
Percent	55.1	38.4	5.8	0.7		6.4	73.2	19.5	0.9	

During this 4-yr period over 9,700 age 1 and older trout immigrated into the pond, hence, migrants accounted for about 70% of total recruitment of yearling and older trout.

It is likely that trout migrating from Elton Creek into Clubhouse Springs were smaller than pond residents because: 1) trout in Elton Creek grew more slowly than those in Clubhouse Springs and 2) permanently marked trout in the pond, i.e. residents, were larger than unmarked trout, which were mostly recent immigrants. From 1968 to 1970 fall fingerlings in Elton Creek averaged 4.2 g and those in Clubhouse Springs were 9.6 g. Fall yearlings in Elton Creek averaged 30 g and yearlings in the pond were 46 g. In spring and fall, marked yearlings in Clubhouse Springs were about 20% heavier than unmarked yearlings. For age 2 trout in spring, marked trout were 58% larger than unmarked ones. I made similar comparisons for ages 1 and 2 trout in Hoglot Springs; differences in sizes among marked and unmarked trout were not consistent and I concluded that migrants were similar in size to pond residents.

Growth

Among populations, mean size attained by trout of a given age was greatest in Clubhouse Springs (Table 7). After the first full year of life trout in

TABLE 7.—Estimated mean annual lengths (millimeters) and weights (grams) of brook trout on 15 April and 15 September. Data from Clubhouse and Hoglot springs were from 1968-71 and those from Maxwell Springs were from 1969-72.

Pond and month	Age 0		Age 1		Age 2		Age 3		Age 4	
	$\bar{L}$	$\bar{W}$	$\bar{L}$	$\bar{W}$	$\bar{L}$	$\bar{W}$	$\bar{L}$	$\bar{W}$	$\bar{L}$	$\bar{W}$
Clubhouse Springs:										
April			126	19	176	55	229	127		
September	105	13	166	49	212	105	276	238		
Hoglot Springs:										
April			107	10	150	31	199	72	241	136
September	88	6	130	26	178	56	226	118		
Maxwell Springs:										
April			106	12	154	38	203	89	264	172
September	89	7	147	34	200	88	246	168	300	284

Clubhouse Springs were from 58 to 90% larger than spring yearlings in Hoglot or Maxwell springs. Although trout in Clubhouse Springs maintained a size advantage over their counterparts in the other ponds after the first growing season, age-specific instantaneous growth rates for all populations were similar. I compared mean age-specific growth rates for intervals of April to September and September to April for ages 1-3 trout. There were no significant differences for similar age trout among populations (t-test $P>0.05$). During summer instantaneous growth rates of trout tended to be highest in Maxwell Springs, but there were no consistent differences during winter intervals.

Growth rates of fingerling trout were inversely related to their density (number or weight) when data from all populations were combined (Table 8). Density of yearling trout also had an effect on growth of fingerlings; correlation coefficients were highest when fingerling growth was related to combined density of fingerlings and yearlings. Effects of density on growth rates of age 1 and older trout were inconsistent. When instantaneous growth rates were used as the dependent variable and density in numbers or weight was the independent variable, correlation coefficients were consistently low (Table 8). When age-specific growth was expressed as mean weight or length in September or weight gain from April to September, correlation coefficients were consistently high (Figure 4). The lack of correlation between instantaneous growth rates and density may have been due to underestimation of mean weights of trout in fall, particularly in Clubhouse Springs. Biases could have resulted from: 1) immigration of trout smaller than pond residents, 2) differential exploitation of faster growing individuals in a year class, and 3) errors in estimating year class densities. The lack of correspondence between instantaneous growth rates and other growth parameters has been noted in other studies (Eipper 1964).

Harvest

Fishing success and harvest of trout were influenced by trout densities and fishing pressure. Maxwell Springs supported the largest trout population in 1969 and 1970 and catch rates were highest (Table 9). Among populations annual catch rates were positively related to spring densities of age 1 and older trout ($r = 0.88$; $P<0.01$). There was a significant correlation between biomass of trout harvested (yield) and the

TABLE 8.—Linear correlation coefficients for growth and density of trout ages 0 to 3 in study ponds. (df = 10; $*P<0.05$, $**P<0.01$.)

Independent variable	Age-group of dependent variable	Instantaneous growth rates	Mean length on 15 Sept.	Mean weight on 15 Sept.	Weight gain Apr.-Sept.
Mean trout biomass (kg/ha) of:					
Age 0	0	−0.62*	−0.59		
Age 1		−0.86**	−0.72*		
Ages 0 and 1		−0.85**	−0.76**		
Age 1	1	−0.08	−0.38	−0.61*	−0.53
All ages		0.13	−0.66*	−0.72**	−0.59*
Age 2	2	0.04	−0.81**	−0.79**	−0.62*
All ages		0.14	−0.72**	−0.68*	−0.48
Age 3	3	−0.05	−0.68*	−0.64*	−0.58*
All ages		−0.07	−0.82**	−0.79**	−0.68*
Mean trout density (no./ha) of:					
Age 0	0	−0.78*	−0.84**		
Age 1		−0.67*	−0.64*		
Ages 0 and 1		−0.82**	−0.85**		
Age 1	1	0.01	−0.57	−0.70*	−0.62
All ages		0.01	−0.66*	−0.77**	−0.63*
Age 2	2	0.06	−0.87**	−0.86**	−0.68*
All ages		0.17	−0.71**	−0.69*	0.46
Age 3	3	−0.09	−0.82**	−0.76**	−0.67*
All ages		−0.12	−0.81**	−0.80**	−0.69*

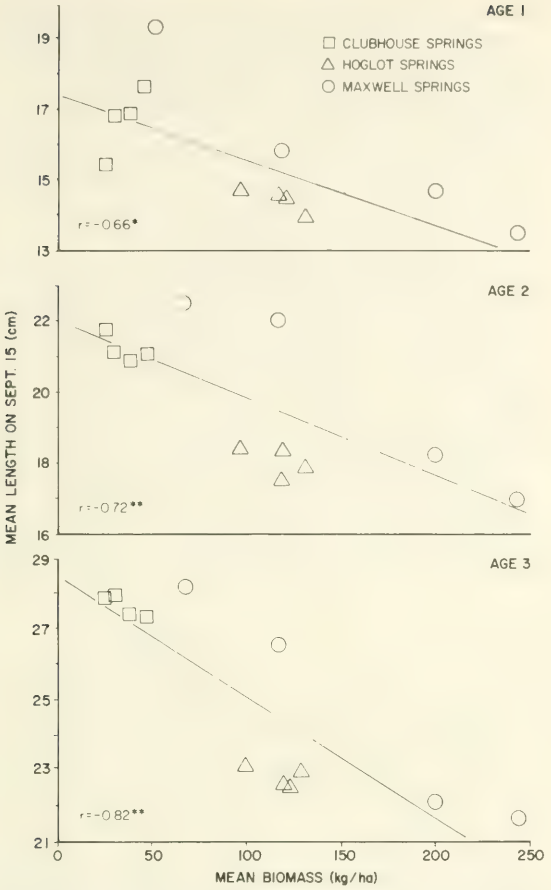

FIGURE 4.—Relationships between mean biomass of all ages of trout and mean lengths of ages 1, 2, and 3 trout on 15 September. (*$P<0.05$; **$P<0.01$.)

TABLE 9.—Annual fishery statistics for brook trout populations in study ponds.

Pond and year	Fishing pressure (angler h/ha)	Total harvest (no./ha)	Catch rate (no./h)	Mean size (cm)	Yield (kg/ha)
Clubhouse Springs:					
1969	1,069	580	0.55	21.8	68.4
1970	1,405	392	0.28	21.4	37.2
1972	809	298	0.37	20.3	27.4
Hoglot Springs:					
1969	835	926	1.11	18.3	54.6
1970	526	391	0.74	19.3	25.4
1972	401	218	0.54	18.8	13.5
Maxwell Springs:					
1969	189	334	1.77	27.2	71.8
1970	154	320	2.08	23.1	39.7

independent variables of fishing pressure and trout biomass in spring ($r = 0.88$; $P<0.05$). Fishing pressure was lowest at Maxwell Springs because the pond was privately owned and public access was restricted. The largest trout (up to 430 mm) were harvested from Maxwell Springs which supported the greatest number of age 4 and older trout. In spring 1969 there were about 530 age 4 and older trout/ha in Maxwell Springs and only 16/ha and 69/ha in Clubhouse and Hoglot springs, respectively.

Age 2 trout made up the major portion of the harvest in Clubhouse and Hoglot springs (Figure 5). In both populations, proportions of age 2 and older trout in the harvest were higher than their proportions in the spring populations, suggesting some size selection by anglers.

The fishery at Maxwell Springs differed significantly from the public ponds in 1969 when age 5 and older trout dominated the catch (Figure 5). Large numbers of age 5 trout were present in spring 1969 and 58% were harvested that season. The owner of Maxwell Springs reported that harvest and fishing pressure in years prior to the study were well below those of 1969 and 1970;

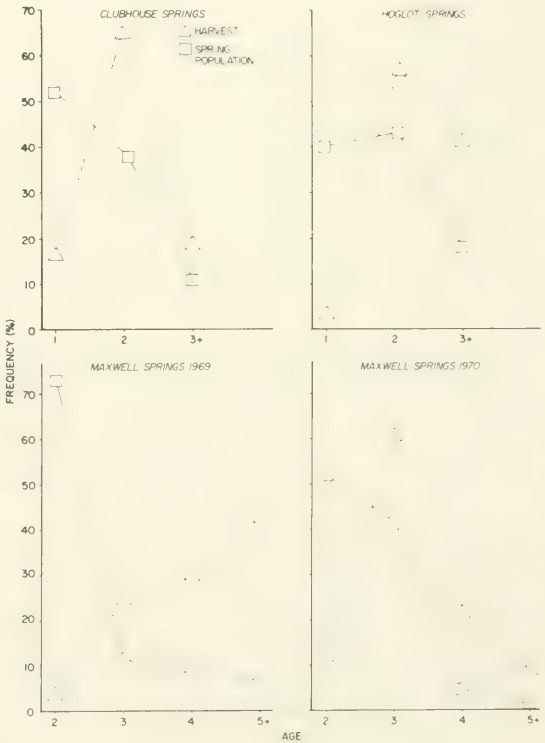

FIGURE 5.—Age-frequency distributions of harvests and populations of legal-sized trout in spring. Data points for Clubhouse and Hoglot springs are means of data from 1968 to 1970, and 1972.

it is likely that the population had been lightly exploited prior to 1969. Results of electrofishing surveys apparently stimulated greater fishing effort. Shape of the 1970 catch-frequency curve resembled those of public ponds, except that substantial numbers of age 4 and older trout were harvested.

Size selection by anglers at Maxwell Springs was reflected in the relative rates of natural and fishing mortality. For ages 2-5 trout, mean total mortality rates from spring to fall increased with age and were paralleled by fishing mortality (Figure 6). Natural mortality changed little with age of fish. Differences between natural and fishing mortality were greatest for age 5 trout and fishing mortality accounted for 69% of their total mortality.

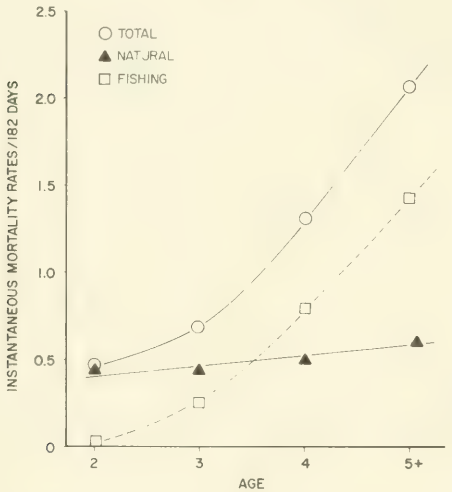

FIGURE 6.—Instantaneous rates of total, fishing, and natural mortality (spring to fall) of ages 2 to 5 trout at Maxwell Springs. Data points are 2-yr means, 1969-70.

Production

Production was most influenced by numbers of fingerlings hatched in ponds and numbers of immigrants. Growth rates varied little among populations, hence year class biomass had the most effect on production. Among populations annual production ranged from 26 kg/ha at Clubhouse Springs to 331 kg/ha at Maxwell Springs (Table 10).

Annual production in Clubhouse Springs was dependent upon biomass of ages 1 and 2 trout. Few fingerlings immigrated into the pond and they contributed only 10% of total annual production. Highest annual production occurred in 1970 when the population was bolstered by high levels of immigration during winter 1969-70 and in summer 1970. Low biomass in spring and below average rates of immigration in 1969 and 1971 resulted in low annual production.

TABLE 10.—Production (kilograms per hectare) by age-group of brook trout in study ponds. Production by age 0 trout during fall to spring intervals covers the period from 1 March to end of interval. Production by age 4 trout includes all older age-groups. Total annual production was expressed in terms of 365 days.

Site and interval	[1]0	1	2	3	4	Total	Annual total
Clubhouse Springs:							
27 Mar. 1968		20.8	11.4	3.9	0.5	36.6	
28 Aug. 1968		1.5	4.4	4.0	—	9.9	45.3
8 Apr. 1969	0.9	5.1	10.8	5.6	1.0	23.4	
8 Sept. 1969		1.8	– 2.0	1.5	0.6	1.9	25.8
1 Apr. 1970	2.7	17.8	9.4	5.5	1.4	36.8	
8 Sept. 1970		5.7	8.7	6.1	0.8	21.3	54.1
29 Apr. 1971	1.0	5.6	5.2	1.8		13.6	
8 Sept. 1971		1.8	7.2	2.7		11.7	25.9
21 Apr. 1972							
Hoglot Springs:							
2 Apr. 1968	40.1	20.9	32.2	10.6	7.9	111.8	
21 Aug. 1968	9.5	2.9	5.6	13.4	–0.3	31.1	141.4
8 Apr. 1969	51.1	21.2	22.7	18.5	4.6	118.1	
8 Sept. 1969	11.3	7.2	3.8	15.5	2.7	40.5	156.4
13 Apr. 1970	56.2	52.9	23.3	11.5	3.0	146.9	
8 Oct. 1970	18.5	6.4	14.7	7.7	1.4	48.7	187.9
28 Apr. 1971	34.8	15.9	35.7	5.9	0.6	92.9	
21 Sept. 1971	14.1	5.1	3.1	10.2	1.3	33.9	125.4
2 May 1972							
Maxwell Springs:							
6 Apr. 1969	97.0	56.8	80.0	17.5	37.0	288.3	
13 Oct. 1969	11.6	10.9	4.9	2.4	1.7	30.2	331.2
26 Mar. 1970	97.5	52.5	38.6	38.7	12.2	239.5	
6 Oct. 1970	34.0	2.8	17.2	20.4	8.6	83.0	297.2
26 Apr. 1971	90.6	17.4	35.3	22.9	6.1	172.3	
20 Sept. 1971	10.6	23.0	1.8	3.1	1.2	39.7	211.4
26 Apr. 1972							

[1]Age at end of interval.

At Hoglot Springs, annual production was most affected by numbers of fingerlings hatched in the pond and numbers of immigrants. Age 0 trout accounted for nearly 32% of average annual production. Annual production peaked in 1970 (Table 10) when large numbers of age 1 trout immigrated oversummer and cohort biomass increased from 13 kg/ha in spring to 91 kg/ha in fall.

Annual production in Maxwell Springs was related to the number of strong year classes present and their subsequent biomasses. The highest annual production was in 1969 when two large age-groups were present (1968 and 1969 year classes), and there was a high biomass of age 2 and older trout (Table 10). In 1971, the year of lowest production, the only large age-group was the fingerlings. In all years, production

of age 0 trout was important; they averaged 44% of the total.

Among populations the influence of age 0 trout on total production was evident when production by individual age-groups was considered in relation to their biomass (Figure 7). Age 0 trout had a marked effect on the slope of the relationship between $\bar{B}$ and P when all age-groups were combined. The linearity of these relationships was due to similarity in growth rates within and among populations. If growth rates had declined with increasing biomass, the relationship between $\bar{B}$ and P would have been curvilinear.

There was no single parameter that could adequately describe levels of recruitment because numbers of trout hatched within ponds and numbers of immigrants were different in each population. If densities of fall fingerlings or spring yearlings were used as indexes of recruitment, mean annual production among populations and recruitment were directly related (Figure 8). Although age 0 trout made up a substantial portion of total production in Hoglot and Maxwell springs, production of just age 1 and older trout was also related to recruitment.

The ratio of annual production to mean annual biomass ($P/\bar{B}$) has been called "turnover rate" and "efficiency of production." The $P/\bar{B}$ ratio is, in fact, the weighted mean growth rate of the population. Population production is the sum of $G \times B$ for each year class, hence, dividing total production by the sum of year class biomasses yields population growth rate, weighted according to the biomass of each age-group.

Among populations annual $P/\bar{B}$ ratios for age 1 and older trout varied by more than 100% (Table 11). The $P/\bar{B}$ ratio in 1969 at Clubhouse Springs (0.63) was probably underestimated. Growth rates

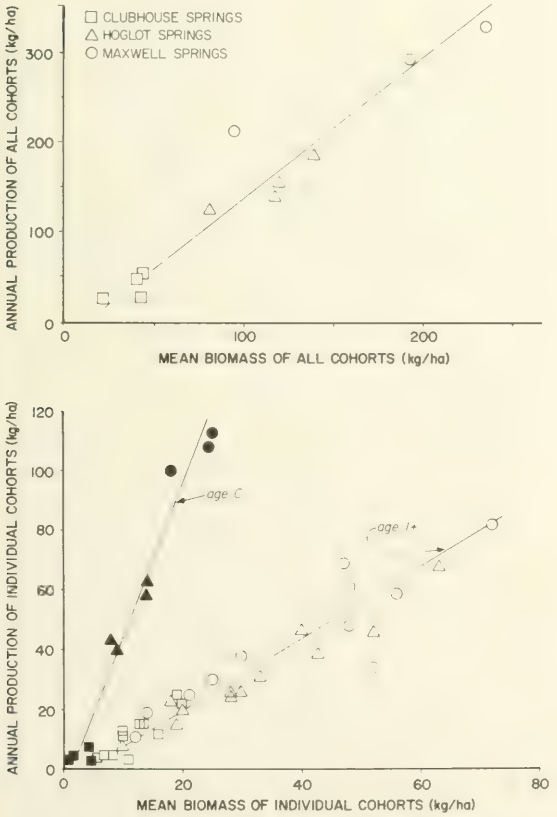

FIGURE 7.—Relationships between mean annual biomass and annual production. Production and biomass of all cohorts are combined in upper panel. In lower panel each point represents a single cohort. Lines fitted by inspection.

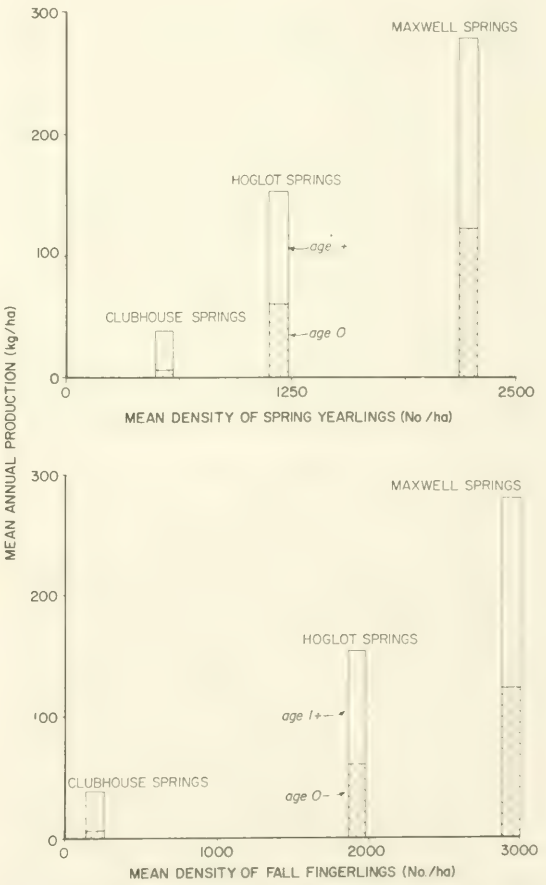

FIGURE 8.—Mean annual densities of spring yearlings and fall fingerlings in relation to mean annual production of age 0 and age 1 and older trout.

TABLE 11.—Total annual production (P), mean biomass ($\bar{B}$), and $P/\bar{B}$ ratios for all age 1 and older brook trout.

Pond and year	P (kg/ha)	$\bar{B}$ (kg/ha)	$P/\bar{B}$
Clubhouse Springs:			
1968	43.4	39.0	1.11
1969	23.0	36.5	0.63
1970	45.7	36.3	1.26
1971	23.0	20.1	1.14
Hoglot Springs:			
1968	89.3	103.1	0.87
1969	95.2	100.0	0.95
1970	110.0	118.2	0.93
1971	71.9	65.9	1.09
Maxwell Springs:			
1969	206.9	199.8	1.04
1970	173.6	162.2	1.07
1971	87.7	64.2	1.37

of individual age-groups during winter 1969-70 were well below average and age 1 trout lost weight. This was the only period in which an age-group in Clubhouse Springs had a negative growth rate, and it was probably due to immigration of yearling trout smaller than pond residents. Overwinter production in 1969-70 was 2 kg/ha; production during other winter periods ranged from 10 to 21 kg/ha.

P/B ratios for age 1 and older trout in Hoglot and Maxwell springs tended to decline with increasing biomass (Table 11), i.e., mean weighted growth rates were inversely related to density. As I have noted, age-specific, instantaneous growth rates (G) were the only growth parameters poorly correlated with density. Biased estimates of G for individual year classes could have obscured relationships with population density, but did not markedly affect mean weighted growth rates when all adult trout were combined.

DISCUSSION

Estimation of trout production in this study required several assumptions and the data should be interpreted accordingly. Major assumptions were: 1) numbers of emergent fry were 80% of total egg production, 2) growth and mortality rates of age 0 trout were constant from emergence to fall, and 3) production could be estimated from the product of G and $\bar{B}$ when immigration occurred.

Chapman (1967) suggested that production of brown trout fry in Horokiwi Stream (Allen 1951) could have been overestimated by fourfold due to errors in estimating egg deposition and emergence. I used fecundity data from two populations of wild brook trout that were collected from ponds in the same watershed as the study ponds. Fecundity differences among populations were probably not large since growth rates of the trout were similar. I assumed that all eggs were spawned because egg retention was insignificant in other stream populations of wild brook trout (Wydoski and Cooper 1966). In addition, I assumed emergent fry represented 80% of total egg production. Percentage of live embryos in individual redds exceeded 80% in my study. Brasch (1949) studied brook trout reproduction in several ponds; he found survival from egg to emergence was 79%. In laboratory experiments, emergence of brook trout fry exceeded 80% when the substrate was composed of 5% or less sand and concentrations of dissolved oxygen exceeded 7 ppm (Hausle 1973). Therefore, I do not believe estimates of egg production or emergent fry seriously biased production estimates.

The assumption of constant mortality rates from emergence to fall represents potentially large errors in production estimates for age 0 trout. Hunt (1966) found that instantaneous mortality rates from emergence in February to June were about 10 times greater than mortality from June to September; he based mortality rates on 90% emergence of fry. To assess the influence of variable mortality rates, I calculated production for the 1970 year class at Maxwell Springs from emergence to October with different mortality schedules. If mortality were five times greater during the first half of the interval than during the second, production would have been 63 kg/ha, and if mortality rates varied by tenfold, production would have been 60 kg/ha. With a constant mortality rate from emergence to October, estimated production was 109 kg/ha. Thus, if there was an initial high mortality of fry, production of age 0 trout could have been overestimated by 50 to 60%, and annual production by all age-groups would have been overestimated by 19%.

Assumptions that instantaneous growth rates were constant from emergence to fall certainly oversimplify growth history of fingerlings, but overall effects of this assumption on production estimates did not appear significant. Hunt (1966) found large variations in monthly growth rates of brook trout from emergence to October; growth rates increased to a maximum in May and then declined the rest of the year. Average monthly growth rates from February through April were not different than those from May to October (t-test $P>0.05$). These periods correspond to periods for which I calculated production by age 0

trout. If changes in growth rates of trout fry in my study were similar to those in Lawrence Creek, then assumptions of constant growth rates are much less serious than those regarding mortality rates.

To estimate production with the Ricker formula ($G \times \bar{B}$) one assumes that no emigration or immigration occurred (Chapman 1967). Effects of emigration on production are similar to those of mortality. Recognition of emigration allows one to demonstrate the fate of production, but does not directly affect calculated values. Immigration, however, can have serious effects upon production estimates. The Ricker formula integrates two simultaneous processes, growth and mortality. Numbers of fish are assumed to decrease exponentially and their mean weights are assumed to change in a similar fashion. When immigration occurs and an age-group increases in number, the Ricker formula treats this increase as an exponential one.

To assess the influence of immigration on production, I simulated three different immigration patterns in which year class density increased from 1,400 trout/ha in April to 3,600/ha in October (Figure 9). Curve B represents an exponential increase in density, i.e., that assumed in the Ricker formula. Production was calculated at monthly intervals and the same growth rate was used for each simulation. If all immigration had occurred in the first half of the interval (A), estimation by the Ricker formula would have underestimated production by 30%, and if trout had immigrated in the latter half of the interval (C), production would have been overestimated by 54%. This increase in cohort size was similar to that of age 1 trout in Hoglot Springs in 1970, the largest increase that occurred in either Hoglot or Clubhouse springs. Therefore, potential errors in production estimates for other intervals would have been less serious.

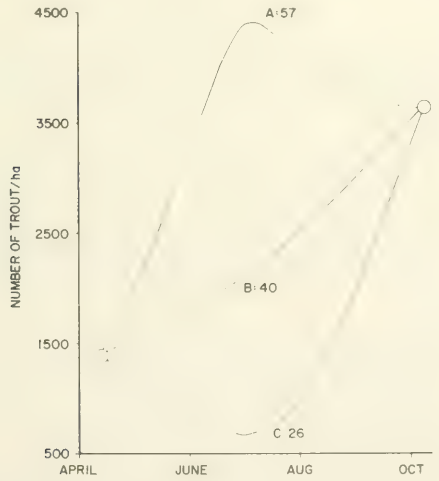

FIGURE 9.—Three hypothetical immigration patterns for a single age-group. Production for each curve was calculated monthly using the same instantaneous growth rate ($G = 0.99$, $t = 0.5$ yr). Total production for each curve is given next to letter designation.

Recruitment, via immigration and spawning within ponds, appeared to be the most important factor influencing production. Even though production by age 0 trout could have been overestimated, production by age 1 and older trout was closely tied to recruitment rates. In other studies, only a few attempts have been made to link production to recruitment. Backiel and Le Cren (1967) analyzed data from Lawrence Creek (Hunt 1966) and Cultus Lake (Ricker and Foerster 1948) and showed that production was directly related to numbers of emerging fry. Highest annual production of sockeye salmon, *Oncorhynchus nerka,* in Lake Dal'neye occurred in years of highest egg deposition (Krogius 1969).

In this study population biomass was determined by annual recruitment. Among populations, production was most influenced by trout biomass because age-specific growth rates were not significantly different. As a result, production increased linearly with biomass. Hunt (1974) found similar linear relationships for brook trout in Lawrence Creek. Backiel and Le Cren (1967) reviewed density effects on production and illustrated both linear and curvilinear associations between production and biomass. Curvilinear relationships resulted when growth rates were severely depressed at high fish densities and in all of these studies fish were stocked and movement was restricted. I am not aware of any study of wild fish populations in which inverse density-dependent growth caused curvilinear relationships between production and biomass. Rather, in wild populations of salmonids, fish densities appear to be maintained at levels that do not result in seriously depressed growth rates and production increases directly with biomass.

Standing crops of harvestable trout (age 1 and older) in the three populations declined over a year's time because total mortality exceeded growth rates, even though immigration bolstered density of some age-groups (Table 12). The actual

TABLE 12.—Comparison of annual yield of brook trout with potential yield and biomass loss to natural mortality. Data are for trout age 1 and older. All values are in kilograms per hectare.

Pond and interval	(1) Annual biomass loss	(2) Annual production	(1 + 2) Potential yield	(3) Actual yield	[(1 + 2) − 3] Biomass loss to natural mortality	Actual potential yield (%)
Clubhouse Springs:						
1970-71	31.0	49.7	80.7	68.4	12.3	85
Hoglot Springs:						
1969-70	27.0	89.0	116.0	54.6	61.4	47
1970-71	8.8	114.5	123.3	25.4	97.9	21
Maxwell Springs:						
1969-70	87.9	200.3	288.2	71.8	216.4	25
1970-71	57.8	188.2	246.0	39.7	206.3	16

biomass loss includes both the change in standing crops from one year to the next and the production during that interval. In all three populations, the actual annual loss in biomass exceeded average standing crops. This loss in biomass may be viewed as the potential yield (Table 12). Biomass lost to natural mortality was calculated as the difference between potential and actual yields. Fate of potential yields appeared dependent upon fishing pressure. In Clubhouse Springs fishing pressure was highest (Table 9), and yield in 1970 was 85% of the potential. Only 16 and 25% of potential yields were taken in Maxwell Springs, where fishing pressure was lowest. The relatively low level of exploitation in Maxwell Springs resulted in substantial biomass losses to natural mortality.

Estimates of fish production in lentic waters have varied from less than 1 g/m^2 to 64 g/m^2, but in most studies they were $<$20 g/m^2 (Le Cren 1972). Highest reported values were for juvenile sockeye salmon in Lake Dal'neye (Krogius 1969). Production estimates for Maxwell Springs (21-33 g/m^2) are among the highest values currently available. Even if contributions of age 0 trout in Maxwell Springs are ignored, production estimates still rank high (11-22 g/m^2). Carline and Brynildson (1977) suggested that high levels of trout production in ponds similar to Maxwell Springs were due to extensive littoral areas and high standing crops of benthic organisms. While prevailing food densities determine the level of potential fish production, attainment of this potential level is dependent upon annual recruitment of some minimum number of fish.

In this study differences in spawning areas among ponds were obvious and trout production varied accordingly. In many instances quantity and quality of spawning sites are unknown or cannot be readily determined. Where recruitment is limiting, fish production will be relatively low, regardless of the water's general productivity. If production is to be used as a measure of a system's capacity to support species of interest, recruitment of that species should be at or near maximum levels.

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KOKO HEAD, OAHU, SEA-SURFACE TEMPERATURES AND SALINITIES, 1956–73, AND CHRISTMAS ISLAND SEA-SURFACE TEMPERATURES, 1954–73

GUNTER R. SECKEL[1] AND MARIAN Y. Y. YONG[2]

ABSTRACT

Sea-surface temperatures and salinities have been collected twice weekly at Koko Head, Oahu, Hawaii, since 1956; and at Christmas Island in the central equatorial Pacific, sea-surface temperatures have been collected daily since 1954. In 1971, Seckel and Yong used harmonic analysis as a curve-fitting method to bring these observations, 1 yr at a time, through 1969, into a form useful for descriptive and numerical applications. In this paper the analyses are updated through 1973 and the method is used to describe the entire data series.

The data series have been separated into several scales of variability: long-term variability (periodicities larger than 1 yr), short-term variability (12-mo and shorter periodicities), average annual cycle (the 12-, 6-, 4-, and 3-mo periods), and the residual variability that characterizes individual years (the short-term variability with the annual cycle removed). In contrast to the Koko Head temperature where the annual cycle predominates, the interannual variability predominates, at times obscuring the annual cycle, in the Koko Head salinity and Christmas Island temperature. The interannual change of the Koko Head salinity can be about three times, and that of the Christmas Island temperature can be about four times the average annual variability. In the average annual temperature and salinity cycles at Koko Head the amplitudes of the 6-, 4-, and 3-mo periods are small in relation to the 12-mo period. In the average annual temperature cycle at Christmas Island, however, the amplitude of the 6-mo period is almost one-half that of the 12-mo period. The residual variations exhibit changing amplitudes and periodicities at intervals of more than 1 yr that resemble amplitude and frequency modulations.

Speculations are made about processes that contribute to the temperature and salinity variations. It appears that in addition to the heat exchange across the sea surface, advection contributes materially to the observed changes at Koko Head and Christmas Island.

Harmonic coefficients resulting from the analyses are listed in the appendices to facilitate reproduction of the data presented.

In an earlier paper, Seckel and Yong (1971) used harmonic analysis as a curve-fitting method, bringing rapidly into usable form regularly sampled sea-surface temperatures and salinities. Analyses were made of sea-surface temperature and salinity obtained once or twice weekly from 1956 to 1969 at Koko Head, Oahu (lat. 21°16′N, long. 157°41′W,), and of sea-surface temperature obtained daily from 1954 to 1969 at Christmas Island (lat. 1°51′N, long. 157°23′W). The temperature and salinity variations for each year were then specified by sets of harmonic coefficients and phase angles. Values calculated at 15-day intervals from the resulting annual functions were used in long-term analyses of the entire data records. These analyses showed that interyear differences in the Koko Head salinity and Christmas Island temperature were larger than seasonal changes.

The long-term changes in surface properties reflect climatic scale ocean-atmosphere processes and, in turn, affect these processes. The changes in properties and processes affect life in the sea. For example, the Koko Head salinity changes indicate primarily changes in the advection produced by variations in ocean circulation (Seckel 1962). It was postulated that changes in circulation also affect the concentration and, therefore, the availability of skipjack tuna caught in Hawaii (Seckel 1972).

The long-term changes in the Christmas Island temperatures are linked with large-scale (at least ocean-wide) ocean-atmosphere processes. Bjerknes (1969) related anomalously high tem-

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peratures and high precipitation at Canton Island in the central equatorial Pacific with intensification of the Hadley circulation and changes in the "southern oscillation." Quinn (1974) related an index of the southern oscillation (the difference of atmospheric pressure between Easter Island and Darwin, Australia) with El Niño phenomena and abnormally high rainfall in the equatorial Pacific. One of the latter is the failure of the Peruvian anchovy fishery. The large interyear differences of equatorial sea-surface temperatures undoubtedly affect the biota in as yet undescribed ways.

It is of value, therefore, to bring the results of monitoring into a form that is useful for fishery applications. Toward this objective we have 1) updated our previous Koko Head and Christmas Island analyses through 1973; 2) analyzed the long series (18 yr for Koko Head, 20 yr for Christmas Island) and separated changes into long-term variability, the annual cycle, and the short-term variability that characterizes individual years; and 3) speculated about the processes that affect the changes evident in the data records.

THE 1970-73 UPDATE

Sampling and Processing

Koko Head, where bucket samples for temperature and salinity determinations were taken twice weekly, is located at the exposed, eastern shore of Oahu. At this location, cliffs extend into the water, and temperature and salinity samples have been found to be representative of offshore conditions. At Christmas Island, bucket temperatures were obtained daily near the plantation village on the ocean side of the lagoon entrance. Measurements were made during the morning at each location.

The procedures used to derive the harmonic coefficients for the 1970-73 observations were the same as those described by Seckel and Yong (1971). Fourier analysis was performed on the residuals from a linear fit so that the temperatures and salinities are expressed as a function of time, t, by

$$S = K + bt + \sum_{n=1}^{k} C_n \cos \omega (nt - \alpha_n) \ldots \quad (1)$$

where $K = F(t_0) + \frac{A_0}{2}$, $\omega = \frac{2\pi}{T}$, and k is the highest harmonic in the series. $F(t_0)$ is the first observed value, A_0 is the Fourier coefficient for $n = 0$, C_n are the coefficients for $n \neq 0$, and α_n are the phase angles. b is the slope of the straight line joining the first and last observations of the fundamental period, T.

The fundamental period for the Koko Head analyses was 365 days. For the Christmas Island analyses the fundamental periods were 120 which for a full year followed in sequence with a 30-day overlap from Julian day 1 to 20, 91 to 210, 181 to 300, and 271 to 390 extending 25 days into the following year.

Results

Results of the analyses for the update years are presented in the appendices. Coefficients and phase angles for the Koko Head temperatures and salinities are found in Appendix A, Tables 1 and 2. Figures of the expected values computed from the harmonic functions together with the observed values for the Koko Head temperatures and salinities are found in Appendix B, Figures 1 and 2. The coefficients and phase angles for the Christmas Island temperatures are found in Appendix C, and the plotted functions together with the observed values are found in Appendix D.

Standard errors of estimate for the fitted Koko Head temperatures and salinities and Christmas Island temperatures are listed in Appendix E, Tables 1, 2, and 3, respectively.

Christmas Island Data Problems

Observer problems at Christmas Island caused the sea temperature sampling to be interrupted from May 1972 to April 1973. The data gap was reduced by Hawaii Institute of Geophysics (HIG) bucket temperatures obtained daily since November 1972 near the airport on the northeast shore of the island. Although NMFS (National Marine Fisheries Service) sampling resumed in April 1973, HIG data were used in our analysis for the entire year. In our long-term analysis the remaining data gap between May and November 1972 was closed by linear interpolation. Mean monthly temperatures obtained from the two sampling sites indicate that NMFS temperatures are on average about 0.5°C lower than the HIG values (Table 1). The HIG data have not been adjusted to reflect this temperature difference.

The large scatter of data at Christmas Island

TABLE 1.—Mean monthly sea-surface temperature (°C), Christmas Island: National Marine Fisheries Service station (NMFS) and Hawaii Institute of Geophysics station (HIG).

	Date	NMFS	HIG
1973	May	26.6	26.2
	June	24.7	25.6
	July	23.6	25.2
	August	23.9	24.5
	September	23.8	24.1
	October	23.4	23.8
	November	23.0	23.3
	December	23.4	23.5
1974	January	23.9	24.0
	February	24.1	24.3
	March	24.6	24.7
	April	24.7	25.2
	May	23.9	24.9
	June	23.6	25.0
	Average	24.1	24.6

in comparison with that at Koko Head indicates another data problem. The scatter probably is caused by sampling of water in the shallow beach area that is more sensitive to changes in the local heating-cooling processes than the deep water of an offshore site.

Finally, there are no systematically observed sea-surface temperatures near Christmas Island against which the shore measurements can be calibrated. However, the monthly pamphlet *Fishing Information*[3] contains a temperature chart for the equatorial Pacific. Contours near Christmas Island are based on insufficient observations to reproduce the temperature distribution reliably. Therefore, the values from these charts, plotted on the annual graphs of Appendix D, show large variations in the difference between the *Fishing Information* temperatures and Christmas Island observations. On average the *Fishing Information* values are 1.3°C higher than the midmonth expected values with differences ranging from −1.2° to 4.1°C.

The discrepancy between the temperature sets, in part, may be due to a tendency toward a warm bias of merchant vessel temperature reports. More probable, however, Christmas Island temperatures, being measured in the morning, reflect the effect of night cooling in shallow water that would be in excess of the temperature decline taking place in deeper, offshore water.

Despite the apparent discrepancies between the beach and offshore temperatures, the data from the shore sampling sites reflect climatic scale anomalies. For example, both the Christmas Island record (Seckel and Yong 1971) and the Canton Island record (Bjerknes 1969) show the equatorial cold anomaly of 1955-56, the warm anomaly of 1957-58, and the anomalous biannual temperature variations of 1963-67.

ANALYSES OF LONG-TERM DATA RECORDS

In this section we present harmonic analysis results of the entire data series and separately display the long-term variability, the short-term variability, the average annual cycle, and the variability that characterizes individual years.

The entire data series is expressed by the function

$$S_L = A + \sum_{n=1}^{k} C_n \cos \omega (nt - \alpha_n) \ldots \quad (2)$$

where A gives the average value of the series, k is the highest harmonic of the analysis, and other symbols have the same meaning as given for Equation (1).

Input values for these analyses were calculated at 15-day intervals from the annual analyses presented in this and our previous paper (Seckel and Yong 1971). Analysis of the 1956-73 Koko Head data was carried to the 72d harmonic and of the 1954-73 Christmas Island data to the 80th harmonic so that the shortest period resolved in each series is 3 mo. Analyses were carried out on the residuals from a linear fit as in the analyses of the annual data sets. The harmonic and linear coefficients for the long-term series are listed in Tables 1, 2, and 3 of Appendix F.

The fitted curves resulting from these analyses together with the input values are shown in panels A of Figures 1, 2, and 3. Dominant in the Koko Head temperature is the annual variation without pronounced longer term trends other than the rise of maximum and minimum temperatures from 1966 to 1968. In contrast to the Koko Head temperature curve, the salinity curve shows longer term variations that are larger than the seasonal variations. Also, during some years such as in 1957, annual variation is not apparent. The Christmas Island temperatures convey a similar picture; interannual changes are larger than the annual changes. Again, the latter may be obscured or absent as during the years 1963-66 and in 1973 when biannual changes dominated.

[3] *Fishing Information*. March 1970 through December 1973. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., La Jolla, Calif.

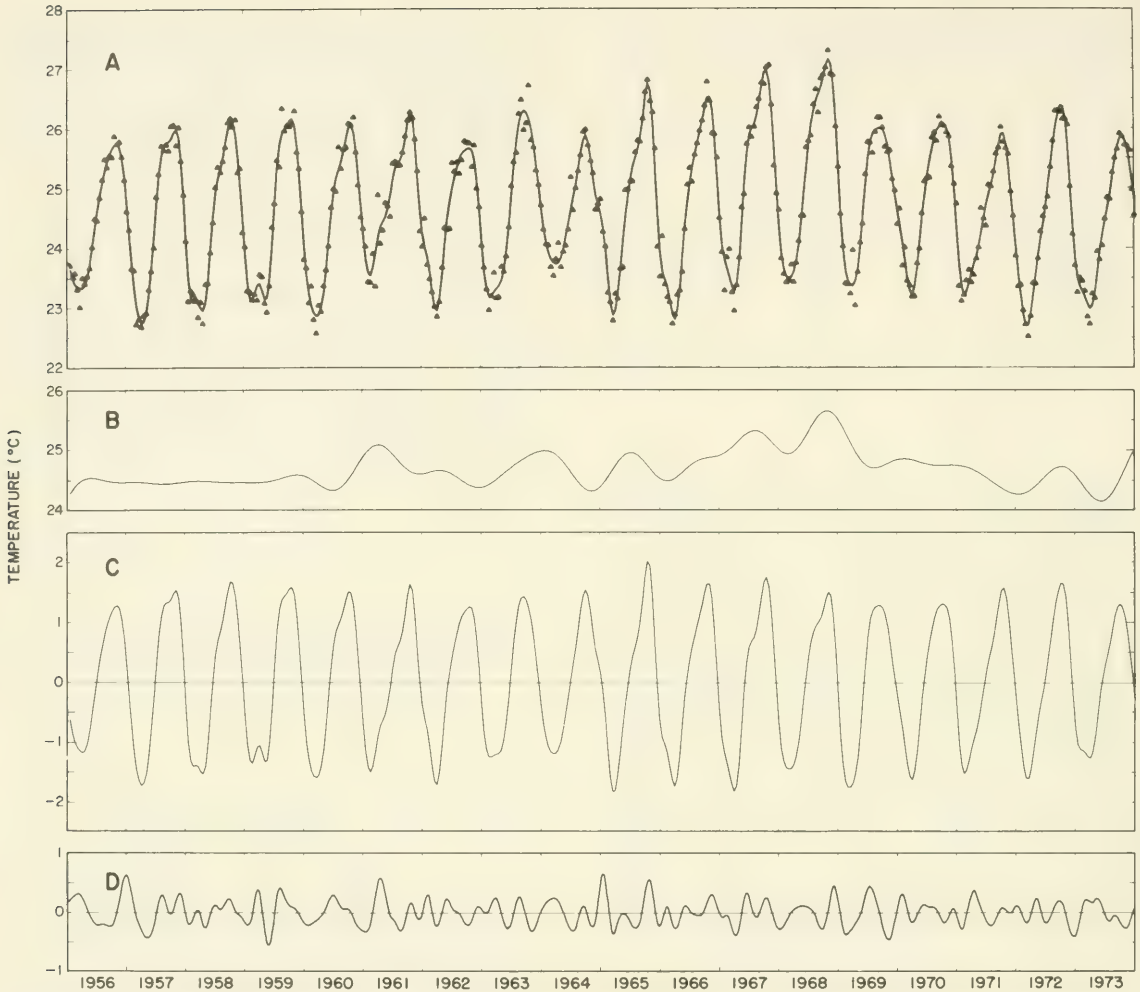

FIGURE 1.—Koko Head temperature, 1956-73: A. Fitted curve with a 3-mo resolution (n = 1-72). B. Long-term variation (n = 1-17). C. Short-term variation (n = 18-72). D. Residual variation (n = 19-35, 37-53, 55-71).

The amplitudes (C_n) of the long-term analyses (Figure 4) confirm these qualitative impressions. In the Koko Head temperature, the amplitude of the annual sinusoid (18th harmonic) is dominant and almost six times as large as the largest amplitude of the long periods. In the Koko Head salinity and Christmas Island temperature, on the other hand, long periods have the largest amplitudes. For the Koko Head salinity the amplitude of the fourth harmonic is larger than that of the annual sinusoid and for the Christmas Island temperature the amplitude of the first harmonic is almost twice that of the annual sinusoid.

Long-Term Changes

When long-term changes are of interest, the annual and shorter term variability can be filtered by a variety of methods including the commonly used 12-mo moving average method. After harmonic analysis has been used as a curve-fitting technique, however, it is simple to evaluate only the terms in the harmonic function up to but not including the annual sinusoid in order to display long-term changes. Thus, in Equation (2), the Koko Head temperatures and salinities were evaluated for n = 1 to 17 and the Christmas Island temperatures for n = 1 to 19. The resulting

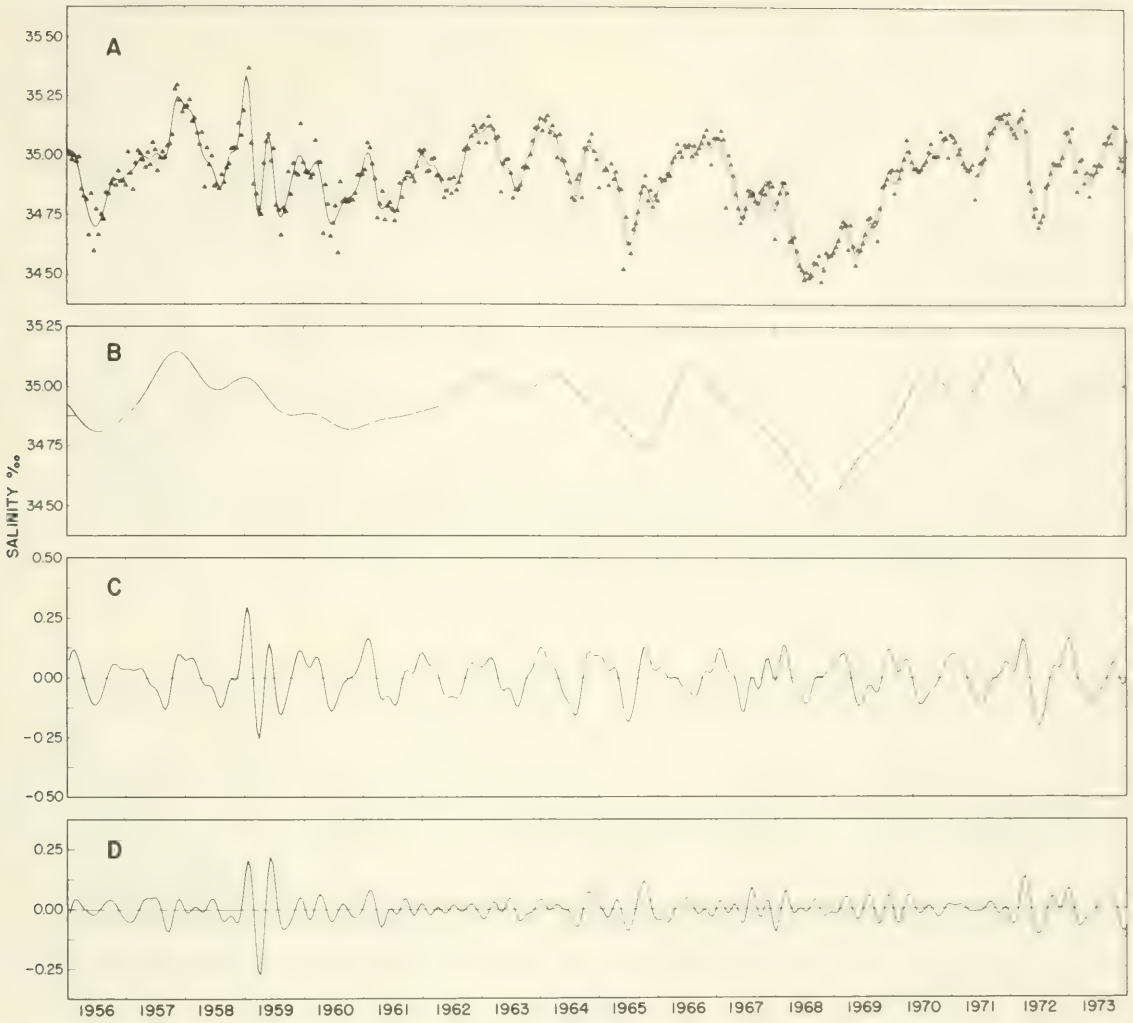

FIGURE 2.—Koko Head salinity, 1956-73: A. Fitted curve with a 3-mo resolution (n = 1-72). B. Long-term variation (n = 1-17). C. Short-term variation (n = 18-72). D. Residual variation (n = 19-35, 37-53, 55-71).

curves are shown in panels B of Figures 1, 2, and 3.

In the Koko Head temperature little variation due to the longer period harmonics is apparent until 1960 when perturbations of 0.5° to 1°C began. A rising temperature trend between 1966 and 1968 was followed by a decline to a pre-1960 temperature level. Both the Koko Head salinity and Christmas Island temperatures show the large perturbations previously noted. At Koko Head a pronounced salinity decline began in 1966, reaching almost 34.5‰ in 1968 before rising again to a range near 35‰. Times of high Christmas Island temperatures stand out. A prominent feature is the pronounced temperature decline during 1973 from one of the highest values to the coldest temperatures observed during the 20 yr of our record.

Short-Term Changes

The short-term changes relative to the long-term trends are another scale of interest that can be obtained by subtracting the moving average or the long-term values of the previous section from the monthly observations. In our case, and

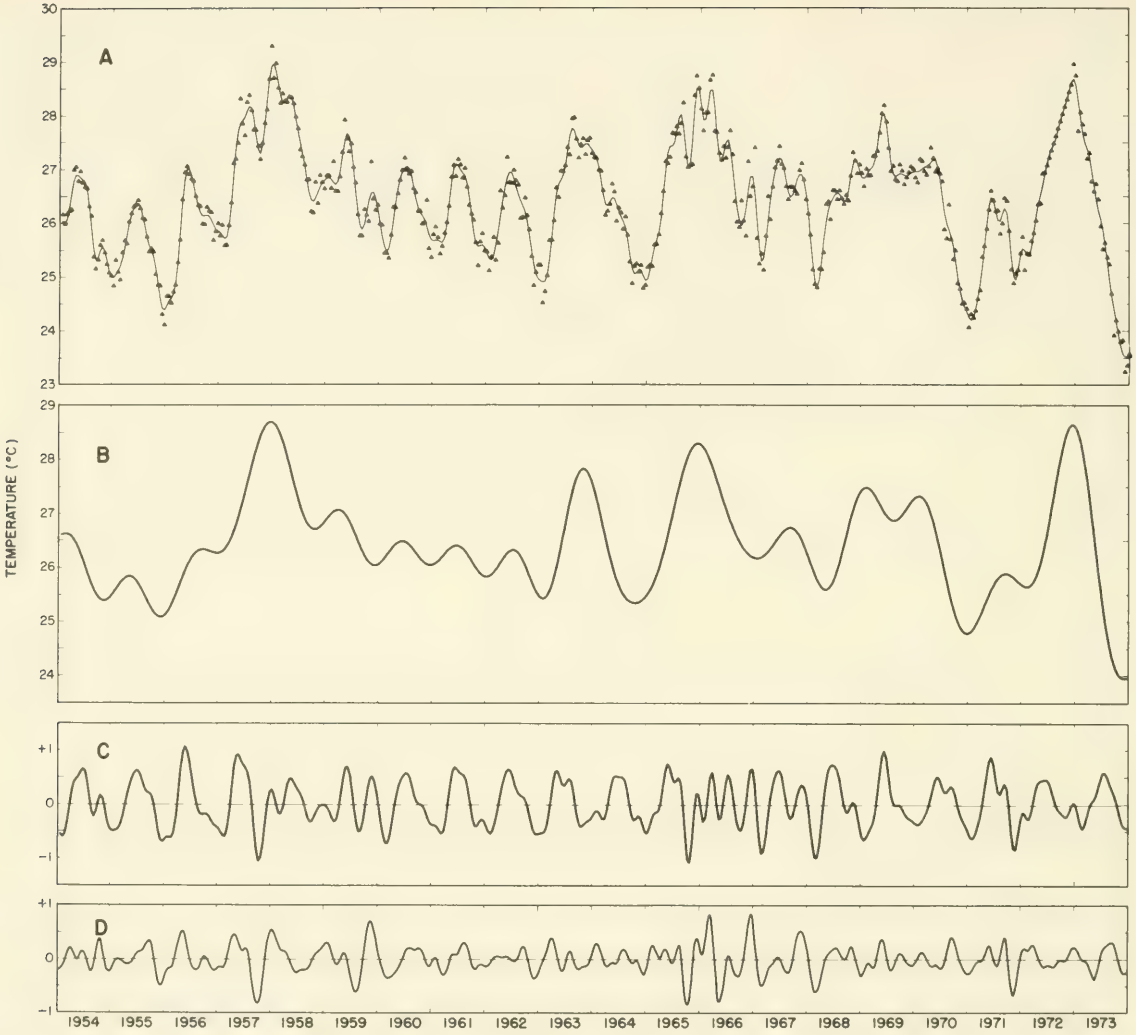

FIGURE 3.—Christmas Island temperature, 1954-73: A. Fitted curve with a 3-mo resolution (n = 1-80). B. Long-term variation (n = 1-19). C. Short-term variation (n = 20-80). D. Residual variation (n = 21-39, 41-59, 61-79).

when variations of <3 mo need not be resolved, it is simple to display short-term changes by evaluating the higher harmonics in Equation (2) beginning with the annual sinusoid (n = 18-72 for Koko Head, n = 20-80 for Christmas Island). The resulting curves are shown in panels C of Figures 1, 2, and 3.

The Koko Head temperature curve looks similar to the initial harmonic fit (Figure 1A) because the long-term changes are small in comparison to the annual variations. In the case of the Koko Head salinity and the Christmas Island temperature, the annual variations that during some years were obscured by the long-term trends are clearly apparent. At Koko Head low salinities occur during spring and summer and high salinities during fall and winter. At Christmas Island high temperatures occur in late spring and low temperatures in fall or winter.

Annual Sinusoid and Its Harmonics

Evaluation of the annual sinusoid and its harmonics yields the mean annual variation. For annual analyses the harmonics n = 1, 2, 3, and 4 have periods of 12, 6, 4, and 3 mo. For the 18-yr

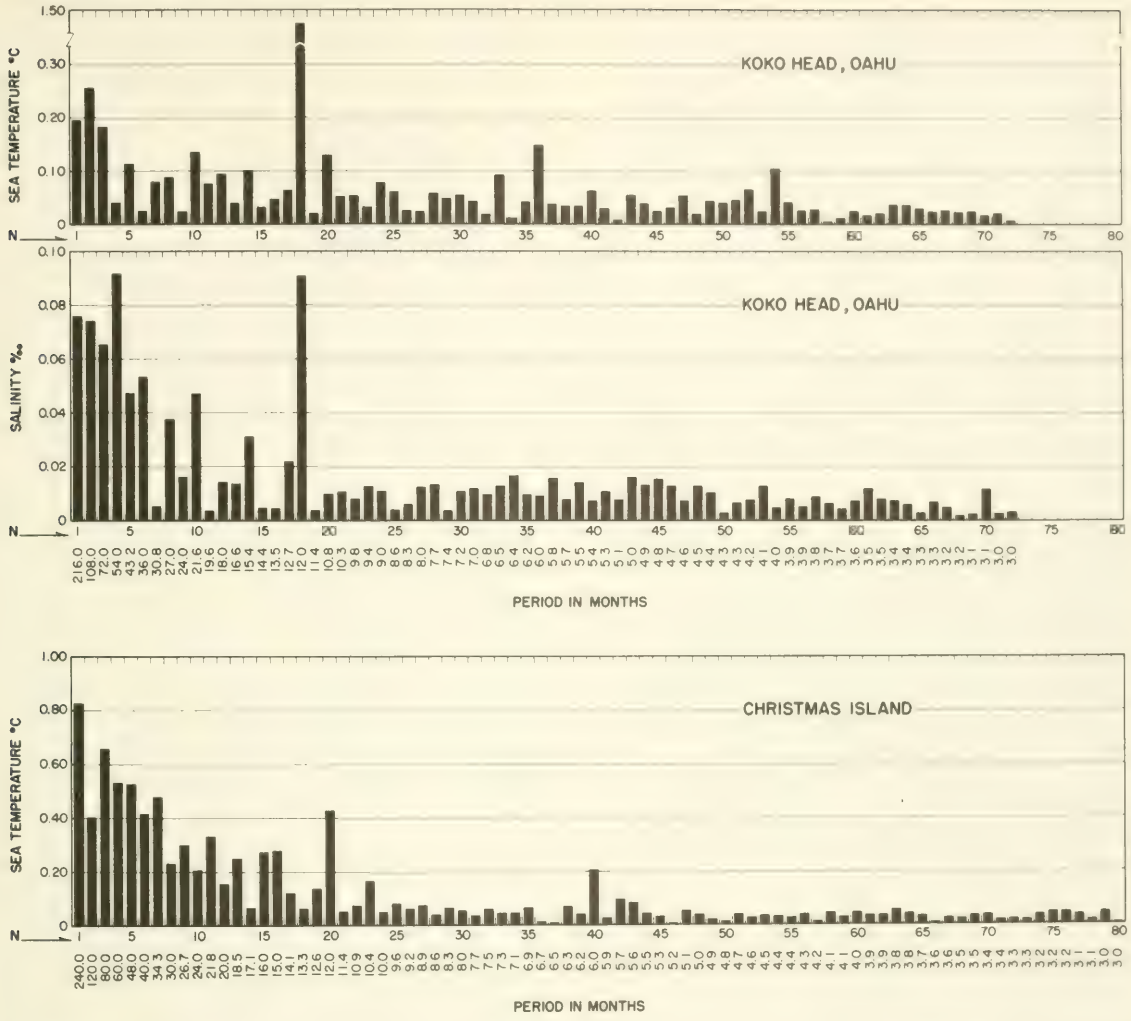

FIGURE 4.—Absolute magnitude of amplitudes of the long-term harmonic functions for Koko Head temperatures, 1956-73; Koko Head salinities, 1956-73; and Christmas Island temperatures, 1954-73.

Koko Head series, these periods are given by $n = 18, 36, 54$, and 72; and for the 20-yr Christmas Island series, they are given by $n = 20, 40, 60$, and 80. The mean annual variations evaluated from Equation (2) are shown in Figure 5 panels A, B, and C.

The mean annual temperature range of 3°C at Koko Head is about twice the long-term range. In contrast, the mean annual salinity range is 0.2‰ and only about 30% of the long-term range. At Christmas Island the mean annual temperature range is 1°C and only one-quarter of the long-term range.

At Koko Head the annual sinusoid, although visibly modified, dominates the mean annual changes. In both the temperature and the salinity, the amplitude of the annual sinusoid is an order of magnitude larger than that of the 6-, 4-, and 3-mo sinusoids (Figure 4). In the case of the temperature, the interference pattern of the 6- and 4-mo sinusoids is such that during the first half of the year the annual sinusoid is not visibly affected. Constructive interference by these sinusoids depresses the annual sinusoid by about 0.2°C in August, which causes first an increase by that amount in October and then a decrease by the end

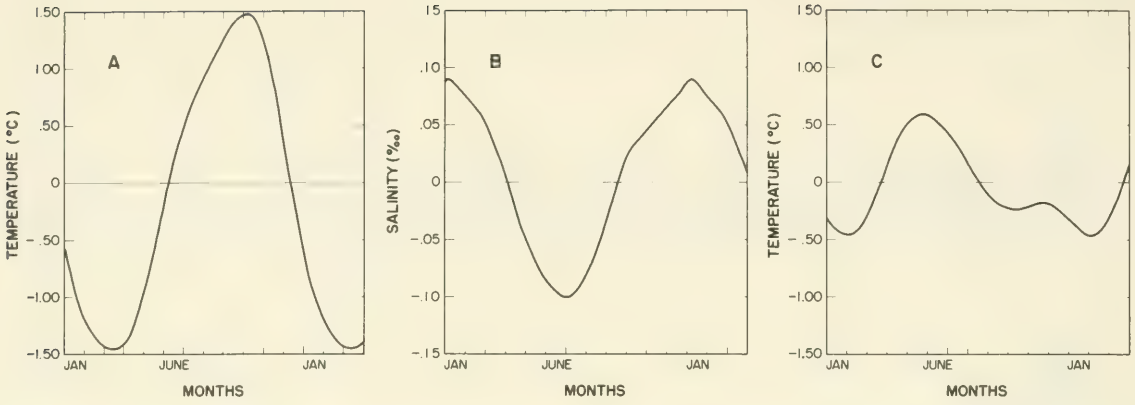

FIGURE 5.—Mean annual variations: A. Koko Head temperatures (n = 18, 36, 54, 72). B. Koko Head salinities (n = 18, 36, 54, 72). C. Christmas Island temperatures (n = 20, 40, 60, 80).

of the year. Consequently, the mean annual curve reflects the temperature trends evident in individual years in that warming lasts between 1 and 2 mo longer than cooling and the cooling rate is higher than the warming rate.

Departures of the mean annual salinity variation from the annual sinusoid, evident in Figure 5B, are not significant.

In contrast to the Koko Head spectra, the amplitude of the 6-mo sinusoid at Christmas Island is large enough to produce a significant modification of the annual sinusoid (Figure 5C). The absolute amplitudes of the 12-, 6-, 4-, and 3-mo sinusoids are 0.43°, 0.21°, 0.04°, and 0.003°C, respectively. Thus, the mean annual temperature variation at Christmas Island has the typical interference pattern produced by a 12- and a 6-mo sinusoid as illustrated in Figure 6. The residual curve, namely the difference between the mean annual curve and the annual sinusoid, is approximately the 6-mo sinusoid.

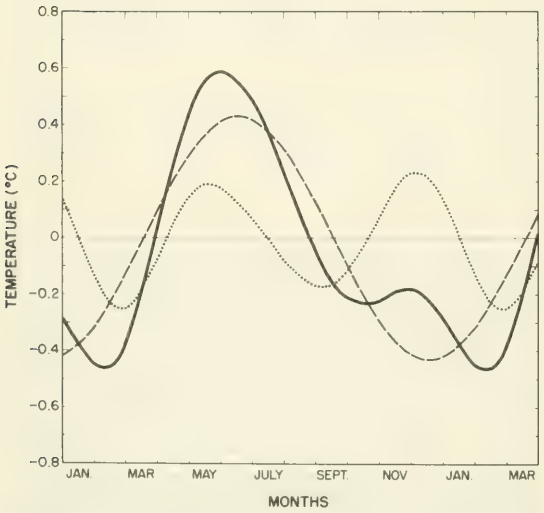

FIGURE 6.—Interference patterns of sinusoids for mean annual variation at Christmas Island. Solid line – n = 20, 40, 60, 80; dashed line – annual sinusoid (n = 20); dotted line – remaining variation (n = 40, 60, 80).

Residual Variations

The dominant feature in the short-term curves (panel C of Figures 1, 2, 3) is the annual variation superimposed upon which is the variability that characterizes each year. This "residual" variability is obtained by evaluating in Equation (2) the short-term variability without the annual sinusoid and its harmonics (n = 19-35, 37-53, and 55-71 for Koko Head, and n = 21-39, 41-59, and 61-79 for Christmas Island). Residual variability is shown in panel D of Figures 1, 2, and 3.

The residual curves are the interference pattern produced by all the sinusoids used in the evaluation. The irregular amplitudes and periodicities occurring at intervals of more than 1 yr give an impression of amplitude and frequency modulations. For example, in the Koko Head salinity curve, relatively large perturbations occur in groups during 1959, 1964-65, 1967-68, 1969-70, and 1972-73. In the Christmas Island residual temperature curve, relatively large perturbations during 1955-60 are followed by smaller perturbations during 1960-65 and by larger perturba-

tions again during 1965-68. These modulations are of a long-term nature but do not appear to be related with the variations shown in panel B of Figures 1, 2, and 3.

On the Separation of Variability Into Various Time Scales

Although there are a number of curve-fitting procedures such as were reviewed by Holloway (1958), we have found Fourier analysis to be a convenient method for the Koko Head and Christmas Island time series. The filtering described above is a byproduct of this method and serves interpretive and descriptive purposes.

Although the moving average method is not recommended for climatological time series,[4] it is commonly used. For this reason, curves obtained by the moving average and the harmonic analysis methods are compared in Figures 7 and 8. The long-term as well as the residual curves of the two procedures are similar though not identical. The amplitudes of the long-term variations are larger in the curves derived by harmonic analysis than in those derived by the moving average method. This difference is to be expected because, in contrast to the harmonic method, input values in the moving average method are weighted equally.

The examples in Figures 7 and 8 were chosen because they illustrate limitations, in terms of physical interpretations, of the filtering techniques. A time series of the sea-surface temperature (salinity) is the signature of processes that govern the observed changes. What information about the governing processes, then, can be inferred from the time series? For example, is the observed change of temperature the result of an anomaly in the local heat exchange across the sea surface and advection produced by the local wind driven current, or is this temperature change a part of a larger scale change with the local processes remaining normal? The examples in panel B of Figures 7 and 8 exhibit variations with an annual periodicity during 1957 in the Koko Head salinity and during 1963, 1964, and 1965 in the Christmas Island temperature although this periodicity is not apparent in panel A of Figures 2 and 3. In these cases were annual variations, such as produced by annually varying processes, present or were they absent?

In the case of the moving average method, 2 yr of data are required to provide the smoothed curve for a single year. At Koko Head the normal mid-year declines in salinity occurred during 1956 and 1958, affecting the shape of the smoothed 1957 curve. Consequently the residual curve showed an annual variation during 1957 (Figure 7B). At Christmas Island (Figure 8B), the residual temperature curve during 1964 also exhibits an annual variation, a maximum in spring and a minimum in fall, although no seasonal trends were indicated during the adjacent years (Figure 3A). In this case, was the normal annual variation in temperature present but obscured by the long-term trend?

In the harmonic analysis procedure the dominant signal in the annual variation is produced by the annual sinusoid. The amplitude of this period is determined by all the data in the series and contributes the same amount to the short-term variations of every year shown in panel C of Figures 1, 2, and 3. For example, a time series could be synthesized by combining a long-term variation with one that has an annual periodicity

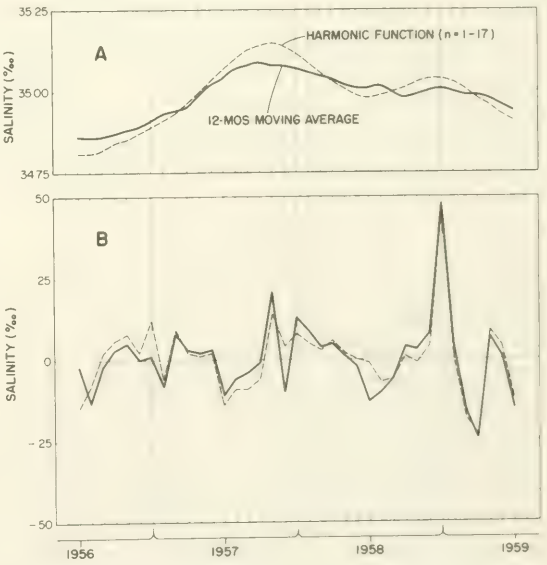

FIGURE 7.—Koko Head salinity, 1956-59: A. Long-term variation produced by 12-mo moving average and by harmonic function (n = 1-17). B. Short-term variation (monthly input values minus long-term values). Solid line — 12-mo moving average; dashed line — harmonic function (n = 1-17).

[4]Climate change. Tech. Note 79, WMO-No. 195, Tp. 100. Secr. World Meteorol. Organ., Geneva, Switz., 1966, 79 p.

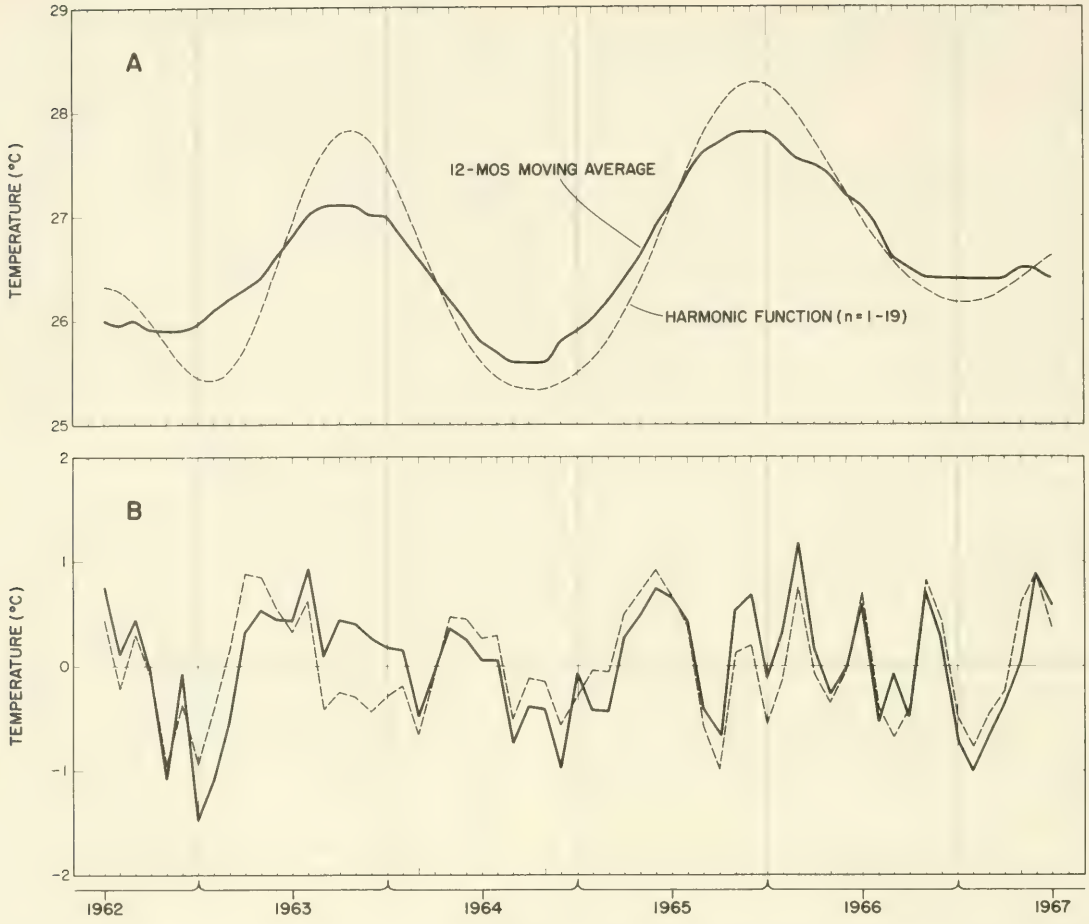

FIGURE 8.—Christmas Island temperature, 1962-67: A. Long-term variation produced by 12-mo moving average and by harmonic function (n = 1-19). B. Short-term variation (monthly input values minus long-term values). Solid line — 12-mo moving average; dashed line — harmonic function (n = 1-19).

every second year. After harmonic analysis and separating the hypothetical curve into a long-term and a short-term variation, the latter would exhibit an annual periodicity during every year.

Thus, the mathematical procedure cannot answer the questions posed above. The procedures illustrated in Figures 7 and 8 as well as other procedures, separate the scales of variability but there is no basis for inferring that the long-term changes are related with, possibly, ocean-wide processes and short-term changes with local processes. Only if the local processes are measured is there a physical basis for the separation into different scales of change.

Speculations About Temperature and Salinity Variations

It is not the purpose of this paper, and the information is not available, to investigate the causes for the temperature and salinity variations that have been described. Nevertheless, such an investigation would further an understanding of the fishery environment as well as the ocean-atmosphere linkages. It is useful, therefore, to speculate about the processes affecting changes in surface properties.

In Hawaiian waters air-sea interaction processes and advection appear to dominate the local

change of temperature and salinity (Murphy et al. 1960; Seckel 1960, 1962). Advection is the product of the surface temperature (salinity) gradient and the component of the current normal to the isotherm or salinity isopleth. Generally near Hawaii the temperature increases and the salinity decreases equatorward. Consequently, with a northward component of flow, advection would increase the temperature and decrease the salinity at Koko Head.

The usual spring salinity decline at Koko Head is best explained by advection. It is estimated that at the latitude of Hawaii there is an excess of evaporation over precipitation with the highest excess occurring during spring and summer (Seckel 1962). Thus, since the salinity is increasing with depth, the only source of lower salinity water lies south of the islands.

On average the orientation of isotherms is northwest-southeast and that of salinity isopleth is zonal. In this case only the meridional component of flow causes salt advection, but both meridional and zonal components of flow cause heat advection. Consequently, meridional components of flow causing salinity variations do not necessarily produce temperature variations. Coincident changes of salinity and temperature that appear to be advection related, tend to occur during late winter and early spring when the North Equatorial Current is weak. For example, between days 60 and 110 of 1973 (Appendix B), decreasing and increasing temperatures corresponded with increasing and decreasing salinities. Pronounced coincident temperature and salinity variations occurred during the first half of 1959 and are most evident in the residual curves, panel D of Figures 1 and 2.

Coincident changes in temperature and salinity during specific seasons are not necessarily associated in the longer term. From 1956 through 1959 when the long-term salinity variations were pronounced, there was no long-term temperature change (panel B of Figures 1, 2). Later, a strong salinity decline lasting from 1966 to 1968 corresponded with a temperature increase. Then, as the salinity returned toward 35‰, the temperature also returned to the pre-1965 values. The first situation may mean that there were climatic shifts in the general northwest-southeast direction, parallel to the isotherms, thus causing a long-term change in the salinity but not in the temperature. In the second situation the climatic shift was first northward and then southward, affecting both temperature and salinity.

White (1975) described secular changes in baroclinic transport and morphology of the North Pacific subtropical gyre and indicated that during the years of low maximum transport the southwest portion of the gyre extended farther south than during the years of large transport. Similarly, it is possible that higher baroclinic flow and tightening of the gyre near Hawaii will result in lower salinity and a relaxation of flow will result in higher salinity. The long-term changes in the Koko Head salinity do not correspond with the changes described by White and are only in partial agreement with the supposition when tested against Wyrtki's (1974) North Equatorial Current index. The supposition, therefore, is in error or, the local wind induced surface flow, superimposed on the baroclinic flow, plays an important part in the long-term salinity changes.

At Christmas Island, in addition to the heat exchange and advection, the effect of wind-induced equatorial divergence is a process affecting the sea-surface temperature. Unfortunately, meteorological observations suitable for the calculation of heat exchange across the sea surface were not made on the island. Estimates made by Wyrtki (1966) and Seckel (1970) indicate the net heat exchange across the sea surface near Christmas Island to lie in the range of about 100 to 300 cal cm^{-2} day^{-1}. Assuming that the heat is distributed through a column of water 50 m deep, this process can produce temperature changes from about 0.6° to 1.8°C/mo. Temperature increases within this range are observed (Figure 3A).

An important term in the net heat exchange is the radiation from sun and sky that is affected in the equatorial region of the central Pacific by large variations in cloudiness (Bjerknes et al. 1969). The effect of such variability is most pronounced in late fall and early winter (Seckel 1970, figure 6). For example, the average net heat exchange near Christmas Island for November 1963 to January 1964 was calculated to be 177 cal cm^{-2} day^{-1}, and for the same months 1 yr later, 274 cal cm^{-2} day^{-1}. The average calculated radiation from sun and sky during the same periods was 372 cal cm^{-2} day^{-1} and 440 cal cm^{-2} day^{-1}, respectively, and accounted for 70% of the interyear difference in the net heat exchange. The Christmas Island water temperature declined in the

first and rose in the second of these years (Figure 3A).

Heat gain across the sea surface cannot produce a temperature decline and, therefore, other processes must affect the temperature. One of these processes is heat advection that, at the Equator, is the product of the zonal current and the zonal temperature gradient. A raft designed for underwater biological observations was set out in February 1964 near the Equator at about long. 150°W and drifted westward 1,084 km (585 n.mi.) in 194 h (Gooding and Magnuson 1967) giving an average speed of 155 cm s^{-1}. A current with the speed of the raft, given a zonal temperature gradient of 0.5°C/10° of longitude, would produce a temperature change of more than 1.8°C/mo. A slower surface current, 30 cm s^{-1}, was observed on the Equator at long. 140°W during April 1958 (Knauss 1960). This current with the same zonal temperature gradient as before would produce a temperature decline of about 0.4°C/mo.

The South Equatorial Current indices presented by Wyrtki (1974) reflect large variability in the zonal current such as cited above. Additionally, monthly charts of sea-surface temperature (Eber et al. 1968) show the zonal gradient at the Equator to range from zero to >1°C/10° of longitude. Advection, therefore, is expected to play a large role in the temperature variations observed at Christmas Island.

Near the Equator the wind field is a key element in the evaporative heat loss, the cloudiness (affecting the radiation flux across the sea surface), upwelling, and in driving the equatorial currents. Quinn's (1974) southern oscillation (SO) index is related to the central South Pacific trade winds. It is not surprising, therefore, to find coherence in the changes of the SO index, Wyrtki's current index, and the Christmas Island temperature. Selecting the pronounced features of Figure 3B, declining SO index values during 1956, 1963, 1965, 1968, and 1971-72 correspond with rising temperatures. Increasing index values during 1964, 1966, and 1970 correspond with declining temperatures. During the first series of years South Equatorial Current speeds are declining and during the second series they are increasing.

SUMMARY

In this paper we have used harmonic analysis to make Koko Head temperature and salinity time series and Christmas Island temperature time series available for descriptive as well as numerical applications.

Time series data can be treated by a number of mathematical procedures in order to elicit important information. Initially, however, the presentation of the data in graphical form is most useful. The graphs in the appendices indicate the nature of the annual variations, and Figures 1, 2, and 3 indicate the nature of the long-term variations.

Although spectral analysis is not the objective of our work, the curve-fitting procedure further serves the descriptive purposes in that it permits separation of the time series into different scales of variability (panels B, C, D of Figures 1, 2, 3). For example, at Christmas Island the interannual temperature variation is as much as four times the average annual variation (Figures 3B, 5C). Equivalent figures of Koko Head salinity show that the interannual change can be about three times as large as the average annual variation.

Results of our analyses are also useful in numerical applications. Coefficients and phase angles (Appendices A, C, F) rather than observed values can be used for further calculations. In this manner the sampling variability apparent in the graphs of Appendices B and D is filtered out and variations of undesired duration can be omitted.

The separation of the time series into different scales of variability is a mathematical procedure and physical inferences must be made with caution. For example, Figures 2C and 3C show an annual cycle during every year although no annual cycle was apparent during 1957 in Figure 2A or during 1963, 1964, and 1965 in Figure 3A. The procedure does not indicate whether during these years the processes producing the annual cycle were absent or whether they were present but obscured by other processes. In another example, a 12-mo and a 6-mo sinusoid combine to reproduce the mean annual temperature cycle at Christmas Island. Again, the procedure does not indicate whether there exists a process affecting the temperature with a 6-mo periodicity.

Available information indicates that advection is an important process affecting the observed temperature and salinity variations. At Christmas Island large changes in the zonal component of the South Equatorial Current appear to cause large variations in advection. At Koko Head changes in the North Equatorial Current (Wyrtki

1974) do not correlate with the salinity changes, and variations in the meridional component of flow appear to cause the seasonal and long-term salinity changes.

On the basis of the long-term temperature curve at Koko Head (Figure 1B) one might conclude that interannual changes in environmental processes are unimportant. The Koko Head salinity curve (Figure 2B) shows such an inference to be incorrect and illustrates the value of monitoring more than one property at a location.

An understanding of the processes governing the temperature and salinity changes is pertinent to fishery management problems. Our speculations about these processes illustrate that good correlations between environmental properties and biological concentrations do not necessarily imply causal relationships. An example is the good correlation between skipjack tuna captures in the eastern Pacific yellowfin tuna regulatory area and central equatorial Pacific temperatures or the southern oscillation index, the skipjack tuna catches lagging about 18 mo.[5] Do these correlations mean that temperatures in the central equatorial Pacific determine larval survival and year-class strength or do they mean that the currents affect the concentration and distribution of skipjack tuna in the eastern Pacific with the temperature variations being ancillary? These questions are important if environmental factors are to be included in fishery population models.

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APPENDIX A

Sea-surface temperatures and salinities, Koko Head, Oahu, 1970-73: Phase angles and coefficients for harmonic functions.

$$S = K + bt + \sum_{n=1}^{k} C_n \cos \omega(nt - \alpha_n),$$

$$\omega = \frac{2\pi}{365} \text{ days}^{-1},$$

t is the time in days beginning with the first day in each year.

APPENDIX A TABLE 1.—Phase angles and coefficients for sea-surface temperatures, Koko Head, 1970-73.

PHASE ANGLES IN DAYS

	N-VALUES												
YEAR	1	2	3	4	5	6	7	8	9	10	11	12	13
1970	72.20	-80.01	52.33	38.44	81.41	50.88	-77.02	18.41	-89.79	85.22	-52.91	74.02	-84.68
1971	62.89	31.68	3.24	22.53	71.72	32.74	66.98	3.50	-10.93	-7.10	87.40	-80.98	-74.60
1972	62.93	21.24	66.54	-63.91	64.06	-70.46	83.06	-57.87	-48.34	-43.74	-8.51	76.71	24.69
1973	72.41	-4.17	-88.28	-59.54	-32.96	-89.25	-83.30	-50.69	57.26	-41.10	-19.01	-74.37	80.19

AMPLITUDES

	N-VALUES													
YEAR	K	B	1	2	3	4	5	6	7	8	9	10	11	12	13
1970	25.5140	-0.0039	-1.8222	0.3590	-0.0552	-0.1421	-0.1264	-0.0868	0.1389	-0.1037	0.0876	-0.0646	0.0463	0.0780	0.0461
1971	24.7393	-0.0014	-1.3848	-0.3917	-0.1076	-0.1512	-0.1155	0.0318	-0.0722	0.0299	-0.1358	0.0295	0.0181	-0.0085	-0.0198
1972	24.4534	0.0003	-1.7160	-0.2903	0.0787	-0.1542	0.1731	-0.0360	-0.0577	0.0270	-0.0318	-0.0655	-0.0336	-0.0226	0.0417
1973	23.7849	0.0036	-1.0235	-0.0600	-0.1372	-0.1433	-0.1347	-0.0319	-0.0484	0.0860	0.0569	-0.0463	-0.0632	0.0468	0.0724

APPENDIX A TABLE 2.—Phase angles and coefficients for sea-surface salinities, Koko Head, 1970-73.

PHASE ANGLES IN DAYS

	N-VALUES												
YEAR	1	2	3	4	5	6	7	8	9	10	11	12	13
1970	75.16	-60.43	16.34	70.03	35.34	30.93	-37.70	-36.82	-26.93	-46.86	-77.26	21.73	-2.76
1971	-51.94	-80.21	-63.27	24.14	-45.10	-73.97	60.91	76.63	-34.16	-67.62	-14.74	36.53	-53.75
1972	9.27	-51.54	-89.46	-72.61	-11.74	-20.48	61.79	78.55	59.38	84.94	10.15	24.89	-24.50
1973	-82.26	88.25	23.40	-17.29	1.01	-27.39	-65.68	-60.90	37.04	90.17	-3.22	-50.96	2.98

AMPLITUDES

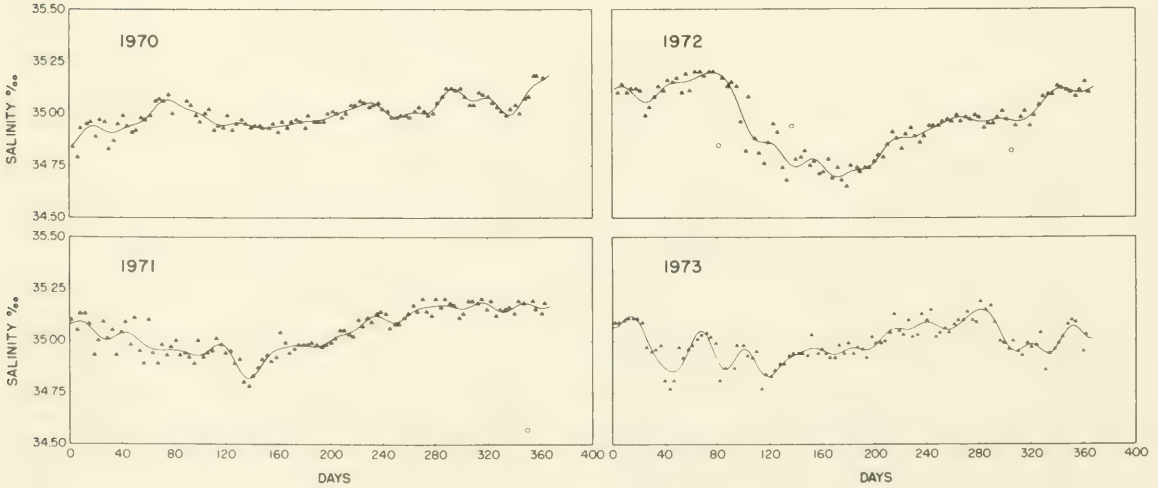
	N-VALUES														
YEAR	K	R	1	2	3	4	5	6	7	8	9	10	11	12	13
1970	34.8321	0.0009	0.0691	-0.0482	-0.0141	0.0196	0.0353	0.0107	-0.0073	0.0024	0.0002	0.0033	0.0059	-0.0115	-0.0105
1971	35.0025	0.0005	0.1115	-0.0132	0.0050	0.0111	-0.0078	0.0208	0.0160	-0.0036	0.0126	-0.0134	-0.0084	-0.0027	-0.0096
1972	34.9629	0.0	0.1838	-0.0807	0.0324	0.0365	0.0209	-0.0133	-0.0010	-0.0046	0.0127	0.0157	-0.0052	0.0089	-0.0085
1973	35.0231	-0.0002	0.0960	0.0213	0.0250	0.0341	0.0401	-0.0057	-0.0190	-0.0220	-0.0207	-0.0270	-0.0018	-0.0116	-0.0175

APPENDIX B

Sea-surface temperatures and salinities, Koko Head, Oahu, 1970-73: Fitted curves with observed values for each year.

Note: Circled observations have not been used in the harmonic analysis.

APPENDIX B FIGURE 1.—Sea-surface temperatures, Koko Head, 1970-73.



APPENDIX B FIGURE 2.—Sea-surface salinities, Koko Head, 1970-73.

APPENDIX C

Sea-surface temperatures, Christmas Island, 1970-73: Phase angles and coefficients for harmonic functions for each quarter of the year.

Days 1 to 120 = First quarter,
91 to 210 = Second quarter,
181 to 300 = Third quarter,
271 to 390 = Fourth quarter, extending 25 days into new year,

$$S = K + bt + \sum_{n=1}^{k} C_n \cos \omega (nt - \alpha_n),$$

$$\omega = \frac{2\pi}{120} \text{ days}^{-1},$$

t is the time in days beginning with the first day of each quarter.

PHASE ANGLES IN DAYS

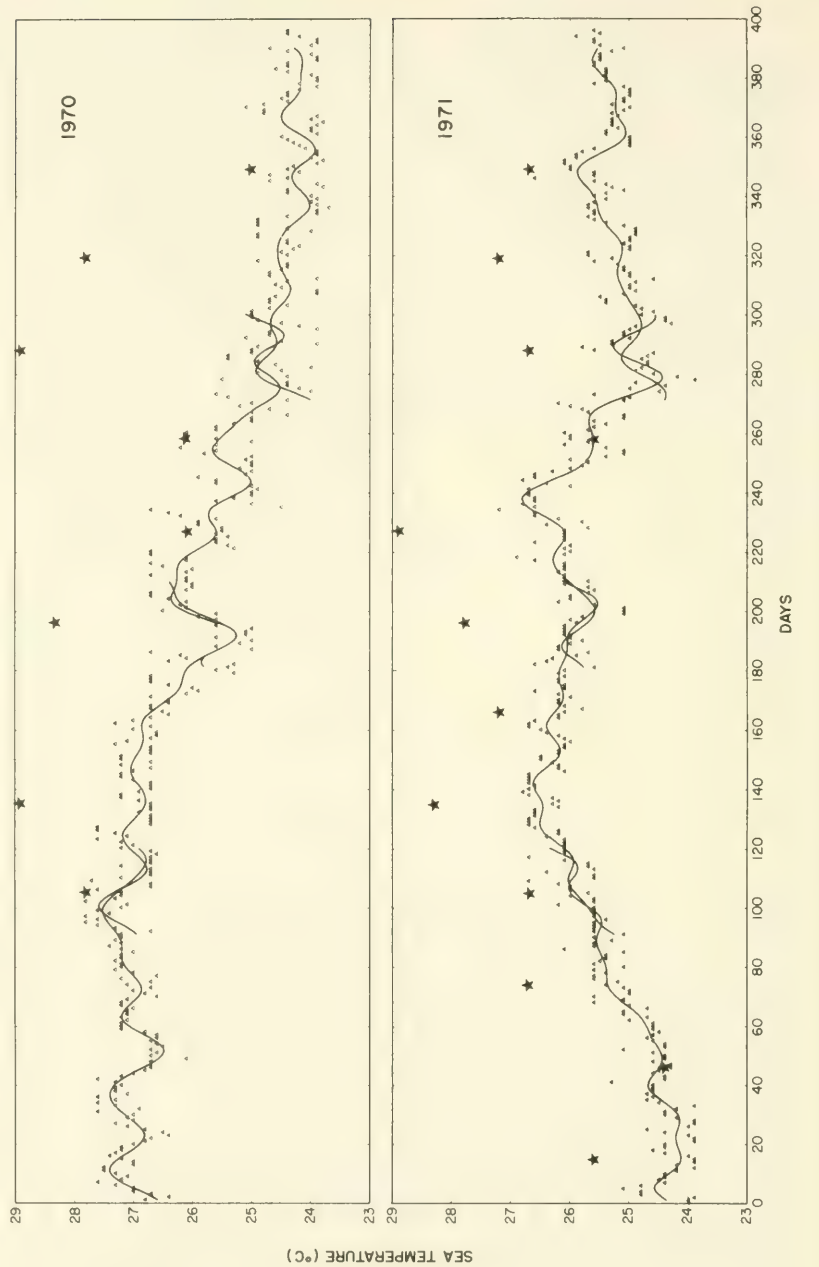
		N-VALUES						
YEAR	QU.	1	2	3	4	5	6	7
1970	1	12.44	-6.13	-16.78	-28.73	-2.68	6.81	16.58
	2	-22.81	17.61	7.60	14.33	0.98	13.65	-6.74
	3	-22.04	-10.25	-16.75	28.25	20.57	9.51	18.38
	4	26.63	-22.46	-18.15	-13.17	25.92	16.12	3.83
1971	1	-9.01	18.72	0.88	-23.22	-19.97	23.78	26.21
	2	-14.62	-11.07	-29.19	-19.30	18.78	-28.63	12.39
	3	-3.95	-4.74	8.40	-13.89	-2.60	-5.65	-26.25
	4	-7.34	24.95	-13.18	3.21	11.76	-16.66	25.18
1972	1	7.89	-27.53	-29.51	-14.94	-26.14	12.85	-22.64
	2	-7.77	-27.22	20.06	4.35	-1.33	21.19	13.69
	3	-6.13	-10.93	-15.60	29.25	28.38	21.23	18.53
	4	1.16	21.36	11.98	1.52	24.55	0.57	-19.27
1973	1	28.56	26.13	9.53	-4.76	-15.17	26.74	24.63
	2	28.96	21.19	12.08	25.17	-8.93	-29.78	-13.43
	3	23.99	-18.26	7.15	-11.40	-29.11	-13.58	16.48
	4	17.68	26.83	-28.88	27.12	-18.74	-21.21	18.01

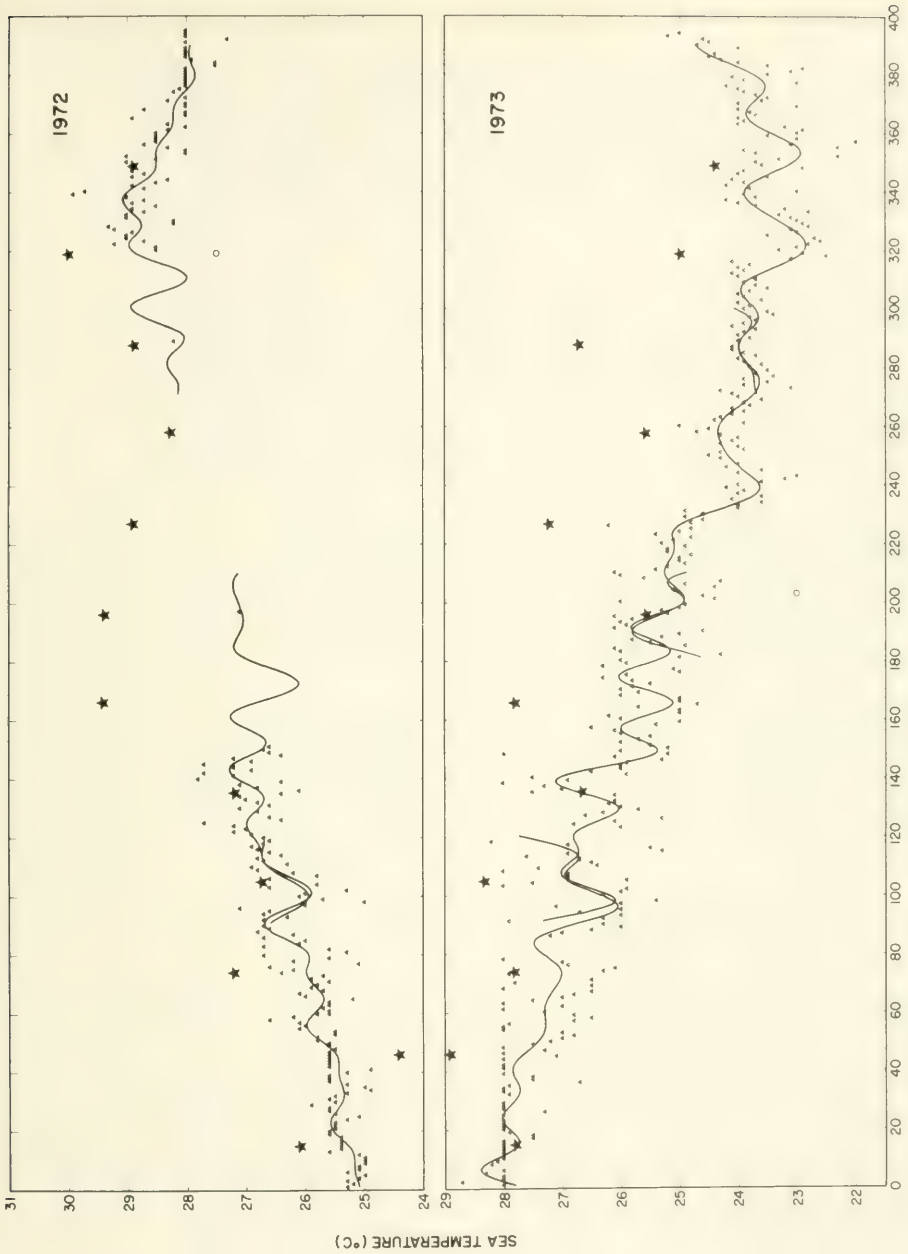
AMPLITUDES

				N-VALUES						
YEAR	QU.	K	B	1	2	3	4	5	6	7
1970	1	26.8641	0.0034	0.0851	-0.1983	-0.0753	-0.2552	-0.1641	-0.0452	-0.1708
	2	26.8841	-0.0041	-0.4763	0.3681	0.1699	0.0824	-0.0936	-0.1911	-0.0469
	3	25.7091	-0.0049	-0.4564	-0.2126	0.1819	-0.0754	0.1993	0.1943	0.1694
	4	24.1813	0.0033	0.3638	-0.1038	-0.1890	-0.0981	0.1659	-0.0722	-0.1883
1971	1	23.9165	0.0176	0.1871	0.0905	0.1300	-0.1024	-0.0435	0.0736	-0.1256
	2	25.6009	0.0083	-0.5389	-0.1219	-0.1488	-0.1029	0.0518	0.0146	0.0775
	3	25.3106	-0.0098	-0.5171	0.2021	0.0472	0.1281	-0.2729	-0.1450	-0.0912
	4	24.6692	0.0091	-0.2184	0.2117	0.0767	-0.1346	-0.0973	0.0931	-0.0717
1972	1	25.0308	0.0133	0.2496	-0.2682	-0.0819	0.1725	0.0821	-0.0718	-0.1126
	2	26.5641	0.0038	-0.1173	0.2415	-0.1913	0.0576	0.2075	-0.1676	0.1283
	3	27.3256	0.0124	-0.2914	-0.5543	0.5778	-0.2516	0.7283	-0.1929	-0.6557
	4	28.5013	-0.0019	-0.3996	0.1060	-0.0935	0.1104	0.1171	-0.1484	0.1384
1973	1	27.2621	0.0017	0.6704	0.3264	0.2433	0.0114	-0.1570	0.2592	0.0925
	2	27.3407	-0.0223	-0.1509	-0.3212	-0.0538	-0.0381	0.1734	-0.0975	0.3913
	3	24.6561	-0.0033	0.6202	-0.2669	0.2438	-0.2662	-0.1172	-0.1534	-0.0632
	4	23.0800	0.0092	0.5485	0.2359	0.1139	0.2976	0.1559	0.1238	0.2243

APPENDIX D

Sea-surface temperatures, Christmas Island, 1970-73: Fitted curves with observed values for each year. Circled observations have not been used in the harmonic analysis. Stars indicate values taken from *Fishing Information*.





APPENDIX D FIGURE 1.— Sea-surface temperatures, Christmas Island, 1970-73: Fitted curve with observed values for each year. Circled observations have not been used in the harmonic analysis. Stars indicate values taken from *Fishing Information* (see text footnote 3).

APPENDIX E

APPENDIX E TABLE 1.—Standard error of estimate (°C) for each annual temperature function at Koko Head, 1970-73, with harmonic analysis carried out in sequence to $n = 1, 2, 3, \ldots$ and 13.

	n-values												
Year	1	2	3	4	5	6	7	8	9	10	11	12	13
1970	0.41	0.32	0.32	0.30	0.29	0.28	0.26	0.25	0.24	0.24	0.23	0.22	0.22
1971	0.37	0.26	0.25	0.23	0.22	0.22	0.21	0.21	0.18	0.18	0.18	0.18	0.18
1972	0.35	0.29	0.28	0.26	0.23	0.23	0.22	0.22	0.22	0.22	0.21	0.21	0.21
1973	0.29	0.29	0.28	0.26	0.24	0.24	0.23	0.23	0.22	0.22	0.22	0.21	0.21

APPENDIX E TABLE 2.—Standard error of estimate (‰) for each annual salinity function at Koko Head, 1970-73, with harmonic analysis carried out in sequence to $n = 1, 2, 3, \ldots$ and 13.

	n-values												
Year	1	2	3	4	5	6	7	8	9	10	11	12	13
1970	0.055	0.043	0.042	0.040	0.031	0.030	0.029	0.029	0.029	0.029	0.029	0.027	0.026
1971	0.047	0.046	0.046	0.045	0.044	0.042	0.040	0.040	0.039	0.038	0.037	0.037	0.036
1972	0.080	0.058	0.054	0.047	0.044	0.043	0.043	0.043	0.042	0.041	0.040	0.040	0.040
1973	0.068	0.066	0.064	0.059	0.052	0.051	0.050	0.047	0.045	0.040	0.040	0.039	0.037

APPENDIX E TABLE 3.—Standard error of estimate (°C) for each quarterly temperature function at Christmas Island, 1970-73, with harmonic analysis carried out in sequence to $n = 1, 2, 3, \ldots$ and 7.

		n-values									*n*-values						
Year	Quarter	1	2	3	4	5	6	7	Year	Quarter	1	2	3	4	5	6	7
1970	1	0.35	0.32	0.31	0.25	0.23	0.22	0.22	1972	1	0.36	0.35	0.35	0.33	0.32	0.32	0.31
	2	0.46	0.37	0.35	0.35	0.34	0.32	0.32		2	Data sets incomplete or missing						
	3	0.50	0.47	0.46	0.45	0.43	0.43	0.42		3							
	4	0.39	0.38	0.36	0.35	0.34	0.33	0.33		4							
1971	1	0.30	0.30	0.28	0.27	0.27	0.27	0.26	1973	1	0.64	0.60	0.59	0.59	0.58	0.55	0.55
	2	0.30	0.29	0.27	0.26	0.25	0.25	0.24		2	0.71	0.68	0.69	0.66	0.65	0.64	0.58
	3	0.42	0.39	0.38	0.37	0.33	0.32	0.32		3	0.53	0.49	0.46	0.42	0.41	0.40	0.39
	4	0.34	0.31	0.30	0.29	0.28	0.28	0.27		4	0.46	0.43	0.43	0.37	0.35	0.34	0.34

APPENDIX F

Harmonic coefficients for the long-term series. Coefficients for each harmonic term in the series

$$S = a + bt + A_0 + \sum_n (A_n \cos n\omega t + B_n \sin n\omega t)$$

are given in the tables below. Harmonic analysis was performed on the residuals from a linear fit. If t is in months, for the Koko Head series, $\omega = \frac{2\pi}{216}$, and the first month in January 1956; for the Christmas Island series, $\omega = \frac{2\pi}{240}$, and the first month is January 1954.

APPENDIX F TABLE 1.—Coefficients for Koko Head temperature. $a = 23.7009$, $b = 0.0020$.

	0	1	2	3	4	5	6	7	8	9
					A_n					
0	0.5478	−0.1755	−0.1397	0.1131	0.0279	−0.0538	0.0263	0.0583	−0.0782	−0.0245
10	0.0174	0.0760	0.0642	0.0401	0.0905	0.0168	0.0439	0.0641	−0.2483	0.0055
20	0.1262	0.0126	−0.0035	−0.0263	0.0408	−0.0211	−0.0253	−0.0235	0.0576	0.0279
30	−0.0428	0.0019	−0.0060	0.0497	−0.0114	0.0191	0.0134	0.0348	−0.0041	0.0258
40	0.0332	0.0042	−0.0024	0.0502	0.0274	0.0056	0.0239	0.0040	−0.0171	−0.0274
50	0.0377	−0.0436	0.0015	−0.0116	−0.1030	0.0298	0.0257	0.0154	−0.0007	0.0068
60	0.0162	−0.0113	−0.0050	−0.0267	0.0202	0.0202	0.0231	−0.0107	0.0145	−0.0234
70	0.0174	0.0117	−0.0067							
					B_n					
0	—	0.0887	0.2135	0.1425	0.0305	0.0989	0.0023	0.0552	0.0418	0.0052
10	0.1329	0.0093	0.0696	0.0044	0.0437	−0.0274	0.0195	0.0056	−1.4540	0.0197
20	0.0262	0.0509	0.0531	0.0198	0.0676	0.0572	−0.0049	0.0035	0.0105	0.0409
30	−0.0313	0.0422	−0.0177	−0.0767	−0.0058	0.0373	−0.1468	−0.0175	0.0347	0.0226
40	0.0519	0.0306	0.0078	−0.0188	−0.0288	0.0258	0.0207	−0.0533	0.0105	0.0327
50	0.0151	−0.0145	0.0652	−0.0230	−0.0113	0.0283	−0.0074	0.0238	0.0050	0.0090
60	0.0188	−0.0138	0.0200	0.0272	−0.0316	−0.0222	0.0053	−0.0254	0.0177	−0.0083
70	0.0011	−0.0167	−0.0020							

APPENDIX F TABLE 2.—Coefficients for Koko Head salinity. $a = 35.0141$, $b = 0.0001$.

	0	1	2	3	4	5	6	7	8	9
					A_n					
0	−0.1228	0.0366	0.0685	−0.0653	−0.0894	0.0441	−0.0034	−0.0048	0.0165	0.0163
10	0.0286	−0.0017	0.0109	−0.0128	−0.0156	0.0024	0.0043	0.0093	0.0903	−0.0020
20	−0.0004	−0.0095	0.0032	−0.0127	0.0017	−0.0035	0.0020	−0.0101	−0.0034	0.0028
30	0.0020	0.0117	−0.0043	−0.0097	−0.0132	−0.0023	−0.0091	0.0094	−0.0067	−0.0039
40	−0.0057	0.0085	0.0070	0.0040	−0.0136	−0.0098	−0.0035	0.0041	0.0030	−0.0053
50	−0.0031	−0.0062	0.0070	0.0130	−0.0002	−0.0092	−0.0053	−0.0002	0.0064	0.0046
60	−0.0006	−0.0048	−0.0039	−0.0021	0.0013	−0.0008	−0.0063	0.0002	0.0014	0.0022
70	0.0089	−0.0016	0.0028							
					B_n					
0	—	0.0663	−0.0287	−0.0063	0.0206	0.0174	−0.0532	0.0026	−0.0221	0.0006
10	−0.0372	−0.0034	−0.0095	−0.0047	0.0268	−0.0041	0.0007	−0.0199	0.0085	0.0034
20	−0.0099	−0.0050	−0.0075	−0.0012	−0.0108	0.0020	0.0058	0.0075	0.0131	0.0026
30	0.0109	0.0028	0.0088	0.0086	−0.0105	−0.0095	0.0021	0.0126	0.0043	0.0138
40	−0.0050	−0.0067	−0.0039	0.0158	−0.0005	−0.0121	−0.0124	0.0064	0.0125	0.0092
50	−0.0002	0.0028	0.0037	0.0001	0.0050	0.0003	0.0001	−0.0089	−0.0003	0.0000
60	0.0074	0.0108	−0.0071	−0.0070	0.0059	−0.0028	0.0028	0.0049	−0.0011	0.0007
70	0.0072	−0.0021	0.0015							

APPENDIX F TABLE 3.—Coefficients for Christmas Island temperature. $a = 26.1443$, $b = -0.0054$.

	0	1	2	3	4	5	6	7	8	9
					A_n					
0	1.5694	−0.2024	−0.3409	−0.1310	0.1924	0.3505	−0.1455	−0.4605	−0.1400	−0.2839
10	0.1658	−0.3162	0.0228	−0.2507	−0.0381	0.1309	0.2614	0.0088	−0.0257	0.0569
20	−0.4204	−0.0517	−0.0635	0.0676	0.0431	0.0179	0.0014	−0.0727	−0.0298	−0.0637
30	0.0295	−0.0316	−0.0583	−0.0133	0.0264	0.0040	0.0073	−0.0021	−0.0587	−0.0397
40	0.1025	−0.0243	−0.0049	0.0496	−0.0108	0.0176	0.0054	−0.0458	0.0351	−0.0144
50	0.0100	0.0321	0.0211	−0.0272	0.0145	−0.0076	0.0085	0.0031	−0.0410	0.0141
60	0.0369	−0.0001	0.0292	−0.0495	−0.0385	−0.0080	−0.0065	0.0232	−0.0204	0.0170
70	0.0134	0.0126	−0.0021	−0.0141	0.0203	−0.0178	−0.0085	0.0325	0.0144	0.0445
80	0.0022									
					B_n					
0	—	−0.8028	−0.2146	−0.6457	−0.4963	−0.3942	−0.3880	0.1339	−0.1839	0.0969
10	−0.1253	0.1038	0.1556	−0.0039	0.0555	0.2400	0.1030	0.1198	−0.0589	0.1246
20	0.0883	0.0041	0.0403	−0.1501	−0.0233	0.0791	−0.0622	−0.0063	0.0252	0.0138
30	0.0456	0.0172	0.0133	−0.0420	−0.0357	0.0625	0.0097	0.0054	0.0347	−0.0026
40	−0.1791	−0.0090	0.0979	−0.0668	−0.0407	0.0247	0.0003	−0.0241	0.0154	−0.0151
50	0.0073	0.0230	0.0144	0.0196	−0.0277	−0.0250	0.0374	−0.0110	0.0054	0.0258
60	−0.0250	0.0336	−0.0219	−0.0223	−0.0124	−0.0314	0.0035	−0.0044	0.0041	0.0267
70	−0.0323	0.0071	−0.0183	−0.0084	0.0289	−0.0417	0.0431	−0.0055	0.0038	0.0022
80	0.0022									

A NEW GENUS AND SPECIES OF EELPOUT (PISCES, ZOARCIDAE) FROM THE GULF OF MEXICO[1]

HUGH H. DEWITT[2]

ABSTRACT

Exechodontes daidaleus n.gen. and n.sp., captured at lat. 27°01'N, long. 84°55'W at a depth of 503 m in the Gulf of Mexico, is described and figured. Its characteristics include the presence of pelvic fins, the absence of scales, teeth on the vomer but not on the palatines, the absence of enlarged canine teeth, teeth on the lateral margin of the dentary and directed outward, grooves behind the upper and lower lips interrupted at the symphyses, the absence of cephalic lateral-line pores, and a greatly reduced lateral line. The new genus appears to be most closely related to the Hadropareinae of the western North Pacific. A key to the genera of the Hadropareinae, including *Exechodontes*, is given.

During June of 1969 the Bureau of Commercial Fisheries (now the National Marine Fisheries Service) RV *Oregon II* was engaged in a survey of shrimp abundance in relatively deep water (360-900 m) in the eastern Gulf of Mexico. Among the fishes captured is one small specimen of a zoarcid which does not appear to belong in any of the currently recognized genera of the family. More surprising, it seems most similar to a group of genera known only from the western North Pacific Ocean.

Exechodontes n. gen.

Type-Species *Exechodontes daidaleus* n. sp.

Diagnosis.—A zoarcid with pelvic fins and lacking scales, with vomerine teeth (two in type-species), but without palatine teeth. No enlarged canine teeth although a few anterior teeth in upper jaw somewhat enlarged; teeth of lower jaw small, in two distinct rows, the outer on the lateral and anterior edge of the dentary such that the teeth are directed outward and are visible when the mouth is closed. Grooves behind upper and lower lips interrupted at symphyses; upper lips not greatly broadened posteriorly. Pores of lateral-line canals absent on head and body; lateral line of body greatly reduced, only a few neuromasts visible close behind head and base of pectoral fin. Head small and without prominent bulging cheek musculature. Pelvic rays long, but only about distal one-fifth of their length bends to extend into the visible fins, the proximal four-fifths lying hidden beneath skin of ventrum. Branchiostegal rays six. Vertebrae with anterior and posterior halves of equal size.

Discussion.—Using various keys to the genera of Zoarcidae (Soldatov and Lindberg 1930; Norman 1966; Lindberg and Krasyukova 1975), *Exechodontes* falls into a group of three genera known only from the western North Pacific Ocean: *Hadropareia* Shmidt (1904) and *Bilabria* Schmidt (1936), both monotypic, and *Davidijordania* Popov (1931) with five species. These three genera constitute the subfamily Hadropareinae (Shmidt 1950), characterized by the absence of spines in the posterior portion of the dorsal fin, the presence of pelvic fins and the absence of crests on the chin (Lindberg and Krasyukova 1975). *Exechodontes* seems closest to *Hadropareia* in that it lacks scales and palatine teeth. *Hadropareia* has, however, distinct pores in the infraorbital lateral-line canal (other pores have not been described or illustrated) and a few pores in the anterior portion of the lateral line which extends posteriorly about three-fourths the length of the body. In addition, *Hadropareia* is described and figured as having the cheek musculature enlarged such that each cheek forms a prominent bulge (Soldatov and Lindberg 1930). *Davidijordania* differs from *Exechodontes* in having scales, palatine teeth and the groove behind the upper lip complete across the snout. *Bilabria* differs in having scales, pores

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in both the cephalic lateral-line system and the anterior part of the lateral line, and the lips of both jaws expanded (Soldatov 1922; Schmidt 1936; Shmidt 1950).

It is possible that the similarities described above are not of real phyletic significance. A. P. Andriyashev (pers. commun.) has pointed out that the Hadropareinae and some other genera (e.g., *Zoarces*) have vertebral centra with the anterior cone shorter than the posterior cone, i.e., the constriction of each amphicoelous centrum is shifted anteriorly. He adds that the Lycodinae, Lycogramminae, and Lycodapodidae have "symmetrical" centra with the constriction placed midway in the length of each centrum. The centra in *Exechodontes* are symmetrical, indicating that relationships may not be with the Hadropareinae (see Figure 3). I have, however, examined radiographs of *Macrozoarces americanus* and *Lycenchelys verrilli* and find that both have "asymmetrical" centra, at least anteriorly. Further analysis of vertebral characters seem indicated.

The following key should serve to separate the four hadroparein genera.

KEY TO THE HADROPAREINAE

1a. Cephalic lateral-line system without pores; outer teeth of lower jaw placed on anterior and lateral margins of dentary and directed outward; scales and palatine teeth absent ..... *Exechodontes* n.gen.

1b. Pores of cephalic lateral-line system present on upper parts of head; no outwardly directed teeth on lower jaw; scales and palatine teeth present or absent 2

2a. Scales absent; musculature of cheek enlarged, forming a prominent bulge along margin of preopercle; palatine teeth absent ..... *Hadropareia*

2b. Scales present; cheek musculature may be slightly swollen, but not forming a prominent bulge; palatine teeth present or absent 3

3a. Palatine teeth present; groove behind upper lip continuous across snout ..... *Davidijordania*

3b. Palatine teeth absent; groove behind upper lip interrupted at tip of snout ..... *Bilabria*

Discovery of a zoarcid in the Gulf of Mexico that has its closest apparent affinities with a small group of genera in the northwestern Pacific is of zoogeographic interest. It is consistent with current thoughts regarding the origin and relationships of several faunal groups of the cooler North Atlantic which also have affinities with the North Pacific. The boreal North Pacific is considered a dominant evolutionary center which provided significant numbers of migrants that invaded the Arctic and North Atlantic during the late Miocene and late Pliocene epochs (Briggs 1974).

Discovery of *Exechodontes* might suggest that there are a number of undescribed species of the family inhabiting the slope waters of the American warm-temperate and tropical Atlantic. The only previously known zoarcid from the Gulf of Mexico is *Lycenchelys bullisi* Cohen which appears to be related to species found in the northern Atlantic and Gulf of Panama (Cohen 1964). Otherwise, the southernmost record for the family in the western North Atlantic is that of *Lycodes brunneus* Fowler from off the east coast of Florida just north of the Bahama Islands (Fowler 1944). In the eastern Atlantic, the family is known south to about lat. 20°N, where two species, probably both misidentified, have been captured at depths between 1,000 and 1,500 m (Vaillant 1888). The pelagic species *Melanostigma atlanticum* has been recorded southward only to the waters off Virginia (McAllister and Rees 1964). It is significant in the present context that *M. atlanticum* is most closely related to the western North Pacific *M. orientale* rather than the eastern North Pacific *M. pammelas* (Tominaga 1971).

Name.—From the Greek *exeches,* projecting, and *odontos,* teeth. The compound is a masculine noun.

Exechodontes daidaleus n.sp.

Holotype.—96.3 mm SL (standard length), collected at *Oregon II* station 10632: 27°01'N, 84°55'W, about 120 n.mi. ESE of Tampa Bay, Fla., in 503 m (275 fm); 124-ft shrimp trawl, dragged on the bottom, 18 June 1969. The specimen (Figure 1) has been deposited in the National Museum of Natural History, Washington, D.C., USNM 211797.

Description.—All measurements are given as

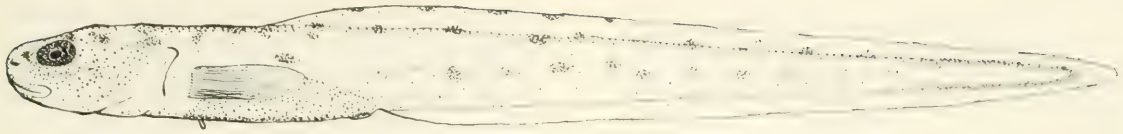

FIGURE 1.—Lateral view of holotype of *Exechodontes daidaleus* n.gen. and n.sp., USNM 211797, 96.3 mm SL.

thousandths of standard length unless otherwise indicated.

Head relatively short, 143 of SL, slightly compressed, its depth and width at cheeks, 78 and 69 of SL. Snout slightly greater than diameter of eye, 39 of SL, very bluntly rounded in both dorsal and lateral views. Nostrils 21 from tip of snout and eye, 36 apart, all of SL, placed at lateral edges of slightly bulbous median part of snout. Eyes placed high on head, but not bulging into dorsal profile, their diameter 34 of SL, placed 38 of SL apart (bony interorbit about 18 of SL). Postorbital part of head 76 of SL. Gill slit moderate, extending ventrally almost to lower edge of base of pectoral fin.

Gape of mouth relatively short, maxilla extending posteriorly to below anterior edge of pupil, length of upper jaw 57 of SL. Teeth all relatively small; those of upper jaw in a single, irregularly spaced row, a few teeth in anterior one third of jaw somewhat enlarged, especially adjacent to symphysis. Teeth of lower jaw in two distinct rows; inner row on dorsal edge of dentary, teeth somewhat irregularly spaced, none enlarged; outer row on lateral and anterior edge of dentary such that teeth are directed outward (most teeth in outer row are missing; cavities in dentary indicate probable tooth positions). Lower jaw included in upper, leaving anterior teeth of upper jaw and outer row of lower jaw visible when mouth is closed. Vomer with two teeth (one missing, but a large tooth cavity present); palatines edentulous. Gill rakers of anterior series of first arch 0 + 0 + 12; those of posterior series 0 + 0 + 11; all are short and blunt. About nine small nubbins present in posterior series of last arch. Pseudobranchiae absent.

Grooves behind lips of both jaws interrupted at symphyses; upper jaw appears to be nonprotractile. Lips narrow, not expanded. No fleshy protuberances or crests present on lower jaw; no cephalic lateral-line pores present anywhere on head (Figures 1, 2). Oral valves present in both jaws, that of lower jaw appearing double, one thin and membranous, lying somewhat anterior and overlying a more fleshy one. Tongue fleshy. Branchiostegal rays six on both sides.

Body slender and compressed, its depth and width 78 and 48 of SL; pectoral to pectoral distance 71 of SL. Lateral line not prominent; a single, prominent, raised neuromast present on each side just above and slightly anterior to upper end of gill slit; a few similar organs (appearing as pale spots) visible in a line curving downwards toward midline behind pectoral fin. Skin delicate but firm on the body. Scales absent. Vertebrae 19 + 78 = 97 (including urostylar vertebra). Vertebrae appear in radiographs to be amphicoelous with anterior and posterior cones of equal size (Figure 3).

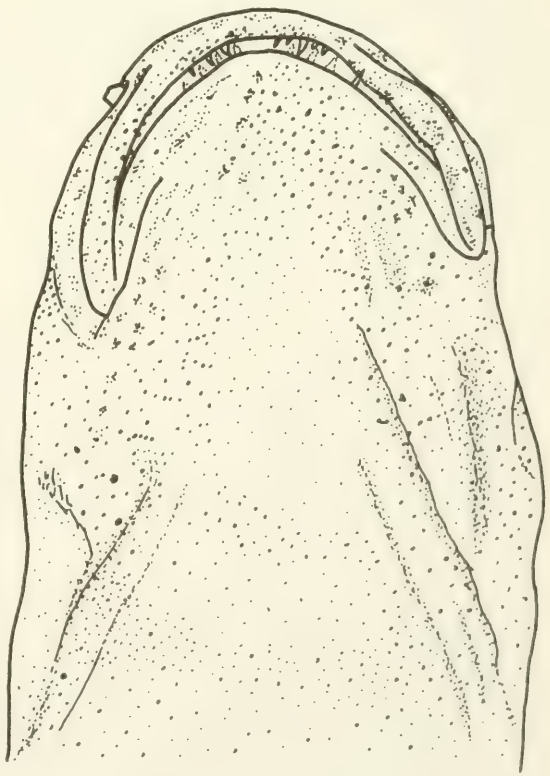

FIGURE 2.—Ventral view of head of holotype of *Exechodontes daidaleus* n.gen. and n.sp., USNM 211797, 96.3 mm SL. Missing teeth in outer row of lower jaw outlined in dots to show presumed position and size.

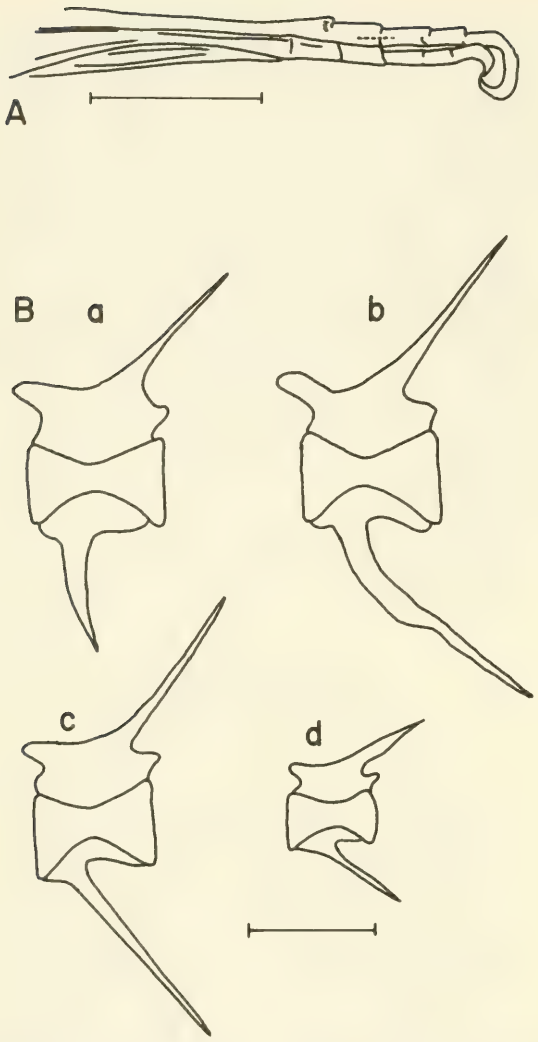

FIGURE 3.—Holotype of *Exechodontes daidaleus* n.gen. and n.sp., USNM 211797. A. Left pelvic rays; the tips originally were straight at about a right angle to main axis. B. Outlines of selected vertebrae traced from a radiograph with the aid of a camera lucida: a, vertebra no. 14; b. no. 20; c, no. 50; d, no. 80. The lines equal 1 mm.

Upper part of small intestine greatly enlarged, about equal in volume to empty stomach. Two very blunt, short and broad pyloric caeca just posterior to thick and muscular pylorus. Gallbladder large and transparent, lying between liver and enlarged upper intestine. A pair of thin gonad chords extending from midway in length of body cavity almost to anus indicate holotype is a male.

Pectoral fins with 15 rays, rounded in outline when rays spread, their length and width of base 104 and 27 of SL, not reaching to above anus. Pelvic fins with two rays, appearing as a pair of small nipples below and slightly behind bases of pectoral fins, their length about 6 of SL. The rays, however, are much longer, 31 of SL, originating anterior to the pectoral fins and lying for most of their length horizontally beneath the skin with only their distal ends bent sharply into the visible nubbins (Figure 3).

Dorsal fin originates behind bases of pectoral fins, above about middle of their length, 235 of SL from tip of snout and 786 from base of caudal fin, with 86 rays. Anal fin originates below base of 12th ray of dorsal fin 341 of SL from tip of snout, 683 of SL from base of caudal fin, and 215 of SL from nipples of pelvic fins, with 79 rays. Caudal fin 38 of SL, with a total of about eight rays.

Color (in alcohol) very pale yellow-brown, almost white, with large, scattered brown melanophores, especially over ventral two-thirds of body which is therefore slightly darker than upper one-third. Small to medium-sized (about 1-3 mm in diameter), irregularly shaped and placed brown spots on upper half of body, rather widely spaced (separated by at least their own diameter). Cheeks and snout darker than body, with more numerous melanophores; brown pigment present in an arc around front of eyes; tip of snout brown. Lower jaw with darker areas of larger and more numerous melanophores. Darker pigment present along bases of posterior parts of dorsal and anal fins, and base of caudal fin. Pelvic nipples brown; pectoral fins with brown pigment. Peritoneum very dark brown, showing through belly as dark blue-grey; viscera pale. Lining of mouth and pharynx pale. Anus ringed with black.

Name.—From the Greek *daidaleos,* dappled or spotted.

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Museum of Natural History very kindly permitted me to examine zoarcid material from the western North Pacific in their care, provided space and facilities for work, and helped in obtaining literature on western Pacific zoarcids.

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SEASONAL MIGRATION OF NORTH PACIFIC ALBACORE, *THUNNUS ALALUNGA*, INTO NORTH AMERICAN COASTAL WATERS: DISTRIBUTION, RELATIVE ABUNDANCE, AND ASSOCIATION WITH TRANSITION ZONE WATERS

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ABSTRACT

In the spring months of 1972-74, fishery-oceanography surveys were conducted in the eastern North Pacific which combined intensive oceanographic sampling by research vessels with concurrent fishing effort for albacore by chartered commercial fishing vessels. The catches demonstrate an association of albacore distribution with the Transition Zone and its boundaries. The relative abundance of albacore was found to be high in the eastern sector of the Transition Zone or a period just prior to their movement across the California Current and into the traditional nearshore fishing grounds. These centers of high relative abundance of albacore are sometimes sufficient to support commercial fishing earlier and farther offshore than the traditional fishing season. Variations in the pattern of migration occur in apparent response to variations in the character and development of the Transition Zone and its frontal structure. Analyses of albacore tagging and size frequency data provide evidence that the shoreward-migrating albacore of the Pacific Northwest and California are independent groups.

The North Pacific albacore, *Thunnus alalunga* (Bonnaterre), is a wide-ranging species which spawns in the central subtropical Pacific, performs transpacific migrations, and supports important commercial fisheries in the western, central, and eastern North Pacific. That marked variations in distribution and relative abundance of albacore occur in the eastern North Pacific is indicated by major latitudinal shifts in the location of the U.S. fishery off the west coast of North America (Laurs et al. 1976). In order to evaluate factors which may affect variations in distribution, relative abundance, and migration patterns of albacore in the eastern North Pacific, and to improve our understanding of the underlying factors affecting the onset and subsequent development of the fishery, early season surveys were conducted in offshore waters of the North American Pacific coast in 1972-74.[2] These surveys found that relative abundance of albacore was high in the vicinity of oceanic fronts of the Transition Zone waters in the eastern North Pacific. Survey results also provide the basis for a hypothesis concerning migration of albacore into coastal waters off the west coast of North America. During these surveys albacore were taken in commercial concentrations farther offshore than traditionally, and several weeks earlier than the fishing season which usually commences in mid-July.

BACKGROUND INFORMATION

Numerous exploratory albacore fishing and albacore oceanographic surveys have been conducted in the central and eastern North Pacific. From surveys conducted during the 1950's, scientists described seasonal variations in distribution of albacore in the central and parts of the eastern Pacific, and demonstrated the association of albacore with Transition Zone waters in the central North Pacific (Shomura and Otsu 1956; Graham 1957; McGary et al. 1961). Flittner (1963, 1964) reported on albacore trolling experiments conducted from U.S. Navy picket vessels operating approximately along long. 130° to 135°W, and presented a schematic model of albacore movement off the Pacific coast (Flittner 1963). Neave and Hanavan (1960) showed that the northern limit of albacore catches made during high-seas salmon gillnetting studies conducted between long. 125° and 175°W was about lat. 45° to 47°N in July and

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[2]These surveys were carried on cooperatively by the National Marine Fisheries Service, Southwest Fisheries Center La Jolla Laboratory, and the U.S. albacore fishing industry through the American Fishermen's Research Foundation.

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lat. 45° to 50°N in August and September. According to Brock (1943), yachts sailing between Hawaii and Oregon during June made albacore catches between lat. 30° and 44°N in waters between long. 154° and 140°W.

Numerous exploratory fishing and oceanographic surveys also have been conducted within a few hundred miles of the coast to obtain information on distribution, availability, and migration patterns of albacore during early season in waters off the Pacific Northwest (Powell 1950, 1957; Powell and Hildebrand 1950; Powell et al. 1952; Schaefers 1953; Owen 1968; Meehan and Hreha 1969; Pearcy and Mueller 1970; and others), and in waters off California (Graham 1959; Clemens 1961; Craig and Graham 1961; and others listed in Clemens 1961 and Pinkas 1963). Johnson (1962), Laurs et al. (1976), and others have discussed variations in distribution and relative abundance of albacore in waters off North America where the U.S. fishery takes place. These studies have shown: 1) the limits of where albacore are found; 2) their general migration patterns; 3) the importance of environmental conditions and changes, notably ocean temperature, in relation to the distribution and relative abundance of albacore; and 4) the considerable annual variation in location of available concentrations of albacore.

In the present study early season albacore surveys were planned to encompass a portion of the eastern sector of the Transition Zone during a period prior to the commencement of the nearshore fishery. The primary objectives of these surveys were:

1) To investigate the early season distribution and abundance of albacore off the North American Pacific coast.
2) To investigate the eastward migration path of albacore entering the American west coast fishery.
3) To determine if migrating albacore are associated with major offshore oceanographic features, particularly the Transition Zone and the ocean fronts that form its boundaries.

METHODS

The general work plan for each offshore survey employed one National Marine Fisheries Service (NMFS) research vessel (*Townsend Cromwell* in 1972 and *David Starr Jordan* in 1973 and 1974) and a group of 5 to 12 commercial albacore fishing vessels on charter to the American Fishermen's Research Foundation (AFRF). The research vessel and chartered fishing vessels worked cooperatively to obtain estimates of distribution and relative abundance of albacore in the offshore area and to make concurrent oceanographic measurements. The research vessel collected physical, chemical, and biological oceanographic data and conducted supplementary fishing activities. The fishing vessels conducted exploratory fishing, tagged fish, and collected surface and subsurface temperature data. The oceanographic findings made on meridional transects were used in directing the exploratory fishing operations, particularly at the onset of each survey. In several instances, especially in 1973 and 1974, the findings of large numbers of fish were used to redirect the research vessel to conduct detailed oceanographic observations in the vicinity.

Operations Aboard Research Vessels

Three meridional oceanographic sections were taken along long. 135°, 137°30′, and 140°W between lat. 31° and 41°N in 1972 and 1973; in 1974 the middle section, portions of the section along long. 135°W, and additional transects were taken (Figure 1). Hydrographic stations were occupied at 25- to 30-n.mi. intervals. Figure 2 shows station positions occupied in 1973; Lynn and Laurs[3,4] gave figures of the station positions for other years. Observations included: 1) salinity-temperature-depth profiles to 500 or 1,000 m using an STD;[5] 2) Nansen bottle or command rosette sampler[6] bottle casts for collection of water samples for determination of dissolved oxygen, chlorophyll, and salinity; 3) oblique zooplankton net hauls and simultaneous surface hauls with neuston plankton nets; and 4) at night stations,

[3]Lynn, R. J., and R. M. Laurs. 1972. Study of the offshore distribution and availability of albacore and the migration routes followed by albacore tuna into North American waters. *In* Report of joint National Marine Fisheries Service-American Fishermen's Research Foundation albacore studies conducted during 1972, p. 10-44. (Unpubl. rep.)

[4]Lynn, R. J., and R. M. Laurs. 1973. Further examination of the offshore distribution and availability of albacore and migration routes followed by albacore into North American waters. *In* Report of joint National Marine Fisheries Service-American Fishermen's Research Foundation albacore studies conducted during 1973, p. 3-35. (Unpubl. rep.)

[5]Plessey model 9006 electronic salinity-temperature-depth profiler. Use of a trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

[6]General Oceanics, Inc.

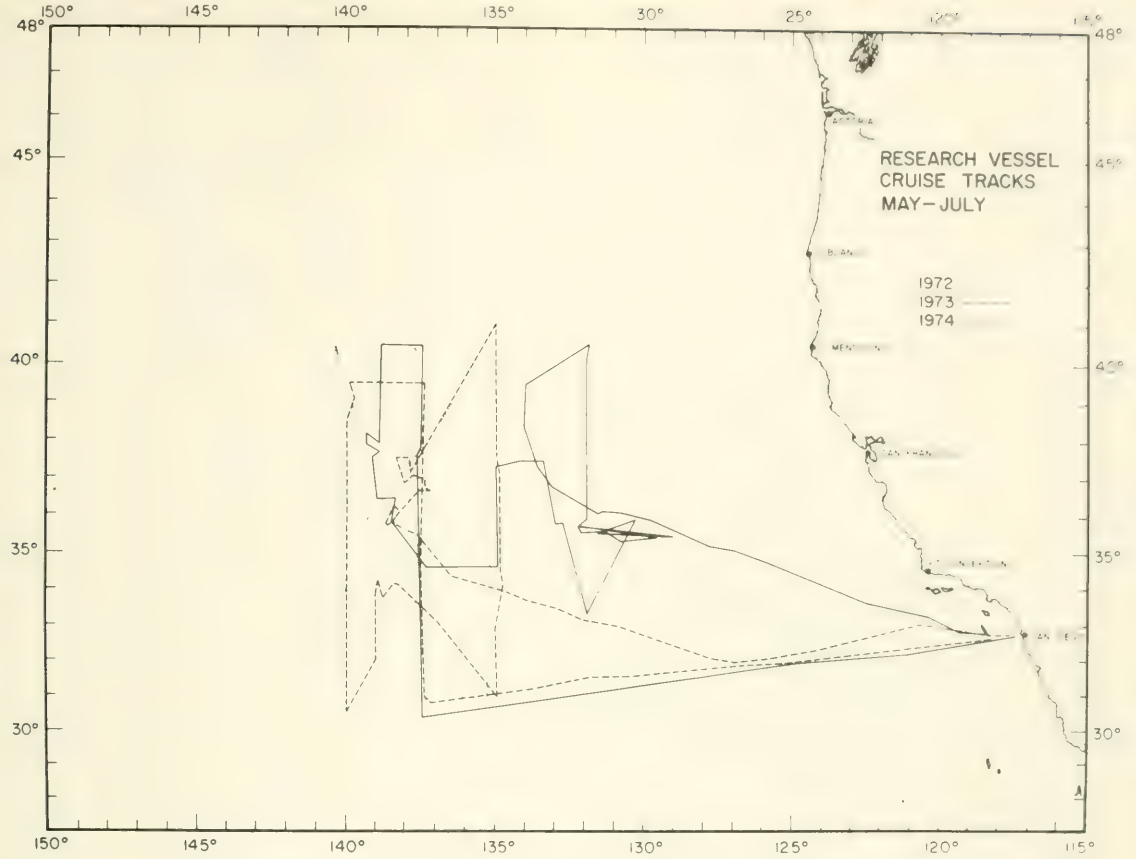


FIGURE 1.—Albacore research vessel cruise tracks for the 1972-74 offshore research surveys.

oblique midwater trawl hauls using an Isaacs-Kidd Midwater Trawl. Also, surface temperature, salinity, and chlorophyll were recorded continuously while underway.

Generally, 10 jiglines (five on *Townsend Cromwell* cruise in 1972) were trolled for albacore on transects between oceanographic stations during daylight. In some regions that were not covered by fishing vessels, trolling was carried on by the research vessel exclusively throughout daylight. On such fishing days, three or four expendable bathythermograph (XBT) drops were made in addition to continuous monitoring of surface temperature, salinity, and chlorophyll.

Operations Aboard Fishing Vessels

The AFRF charter vessels which took part in the offshore surveys were jigboats, except for two baitboats in 1973 which were outfitted to conduct either live-bait fishing or jig fishing. Twelve fishing vessels participated in the operations in 1972 and 1973 and five in 1974.

The fishing vessels sailed in groups of four from San Diego, Calif., and Astoria, Oreg., at 15- to 20-day intervals during 1972 and 1973, and all vessels sailed together from San Diego in 1974. The vessels usually worked in pairs. A schematic diagram of the cruise tracks for the 1972-74 offshore surveys is shown in Figure 3. Detailed cruise tracks showing daily positions and locations of XBT stations for each fishing vessel or pair of fishing vessels by 10-day period are given in Lynn and Laurs[7] (see footnotes 3 and 4).

[7]Lynn, R. J., and R. M. Laurs. 1974. Cooperative NMFS-AFRF early season offshore studies conducted during 1974. *In* Report of joint National Marine Fisheries Service-American Fishermen's Research Foundation albacore studies conducted during 1974, p. 3-18. Southwest Fish. Cent. Admin. Rep. LJ-74-47.

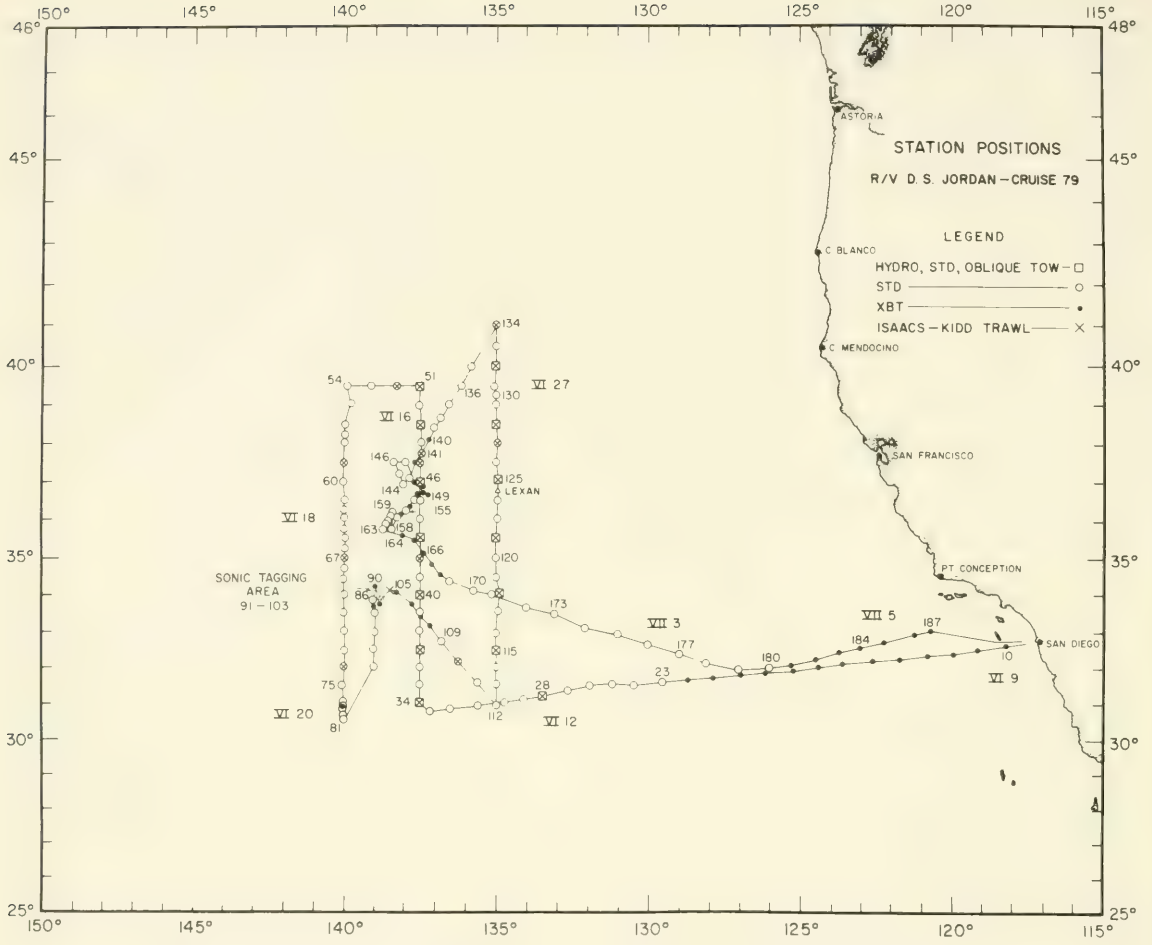


FIGURE 2.—Track and station positions for RV *David Starr Jordan* cruise 79, 9 June-6 July 1973.

Standard commercial albacore fishing equipment and regular commercial fishing methods were used. Most of the jig vessels trolled 10 lines and baitboats 6 or 8 lines when jig fishing. (Baitboats had better success when trolling than when baitfishing.) Daily records pertaining to fishing operations were maintained aboard each vessel, including number of fish caught, fork length of most fish caught (except for two vessels in 1972), positions where fishing was started and ended, amount of fishing effort expended, and fishing conditions and signs of fish. In addition, sea-surface temperature, sea conditions, and surface weather conditions were recorded. Half of the fishing vessels chartered in 1972 and 1973, and all in 1974, were equipped with an XBT system; generally one or two XBT probes were launched each day. Sea-surface temperature measurements were made using bucket thermometers.

EARLY SEASON DISTRIBUTION AND RELATIVE ABUNDANCE OF ALBACORE IN OFFSHORE WATERS

Distribution of Catches Made By Charter Vessels

Nearly 27,000 albacore were caught by the chartered fishing vessels during the three offshore surveys (Table 1). In all three surveys, albacore were taken in substantial numbers in an offshore region between lat. 31° and 36°N from late May through June. Catch rates were generally low or zero in surrounding regions and during explorato-

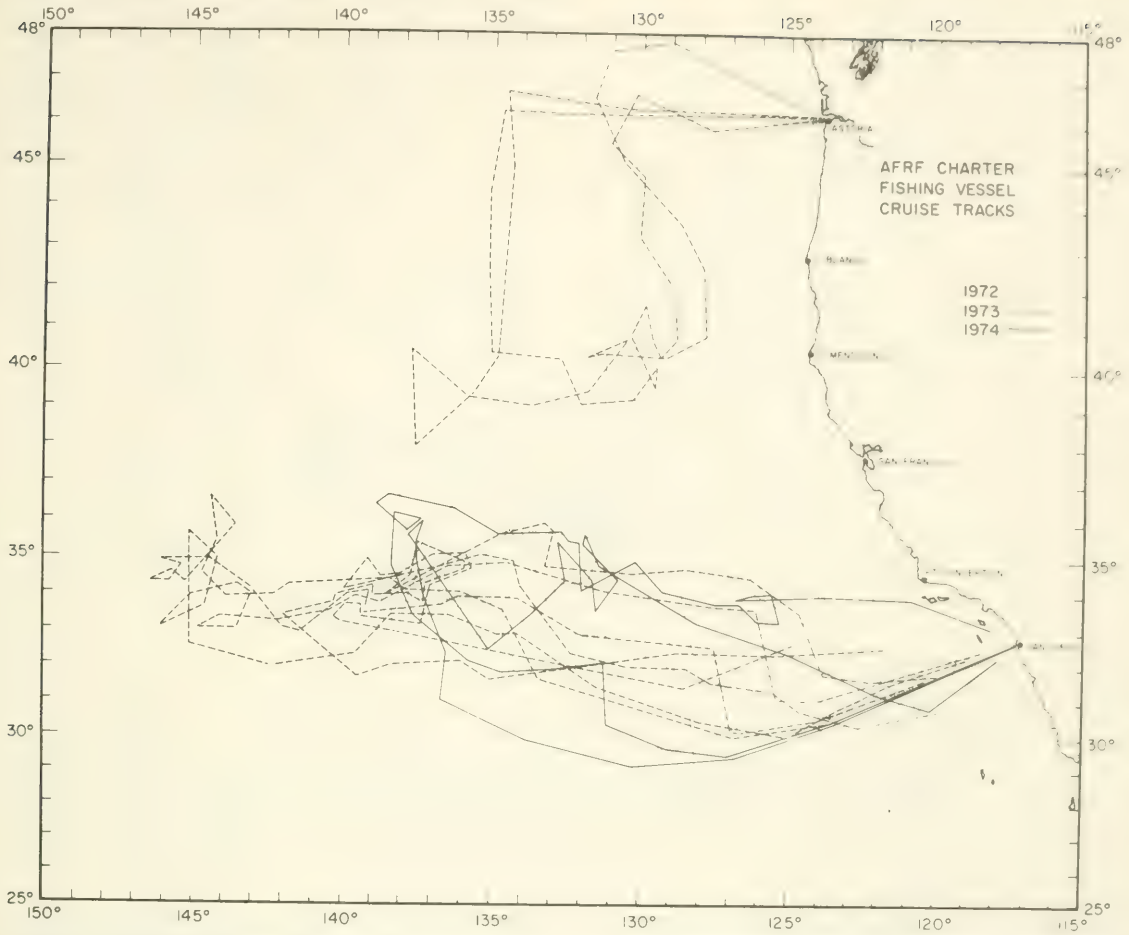


FIGURE 3.—American Fishermen's Research Foundation charter fishing vessel cruise tracks for the 1972-74 offshore research surveys.

ry fishing before late May. Variations in distribution and relative abundance of albacore were observed within and between surveys.

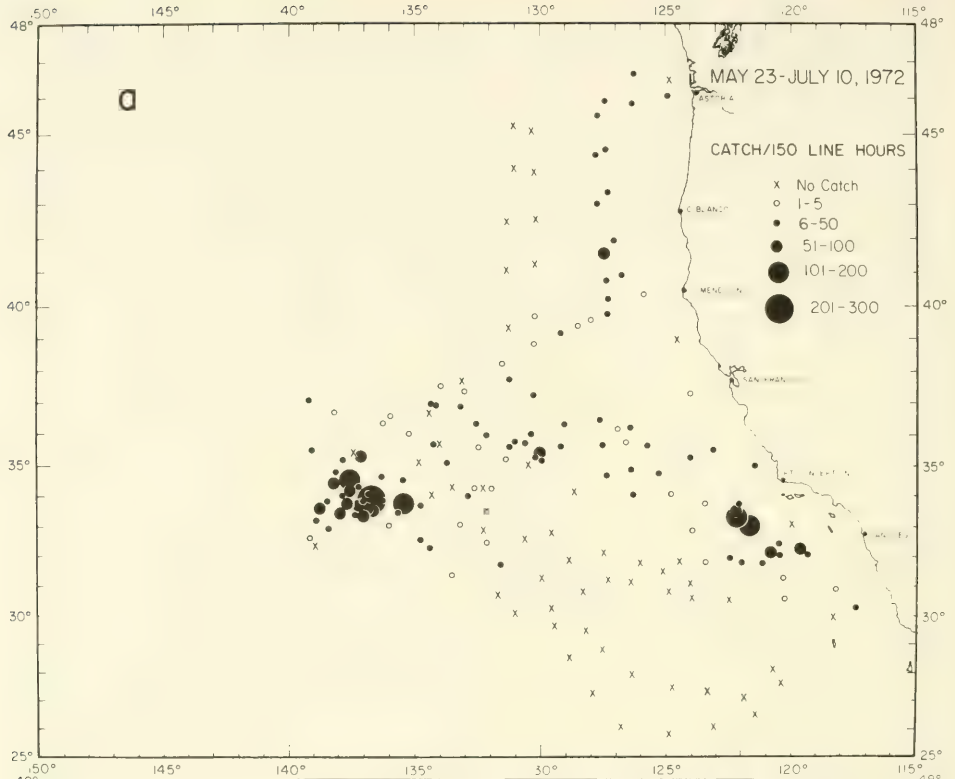
Differences Between Surveys

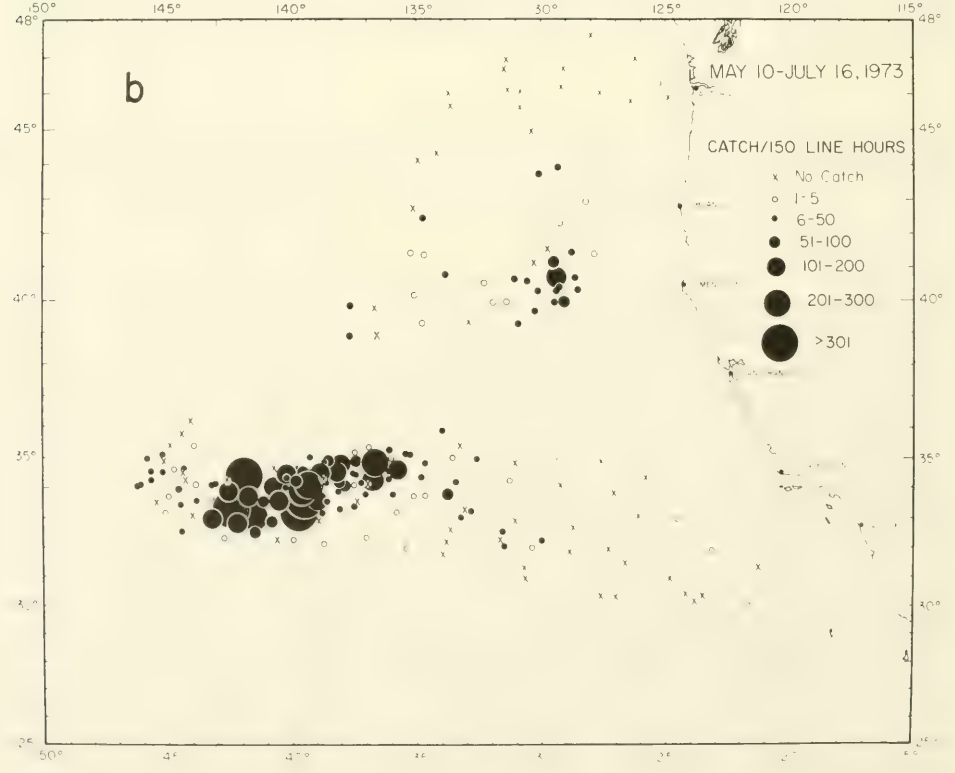
Plots of the charter vessel catches for each survey are given in Figures 4a-c. The catches represented in these and other plots have been standardized to the number of fish caught per 150 line-hours (averaged between pairs of vessels that fished together for 1972 and 1973) and presented graphically by proportionately increasing size of dots.

In 1972 and 1973, relative abundance of albacore was high between lat. 32°and 35°N, long. 135° and 140°W, and lat. 32° and 35°N, long. 135° and 143°W, respectively (Figure 4a-b). In both of these years small or no catches were made in the region between long. 135°W and inshore waters within 150 mi of the coast where fishing takes place during the traditional albacore fishing season. In 1974 (Figure 4c), high catch rates were again made offshore of long. 135°W, but over a larger latitudinal range, lat. 31° to 36°N, and somewhat more scattered than in the two preceding years. Also, high catches were made at about lat. 33° to 36°N, long. 124° to 135°W in the region between

TABLE 1.—Albacore survey catches.

Year	Total catch by charter vessels	Tagged and released	Total catch by research vessel
1972	6,746	1,431	155
1973	11,027	1,738	130
1974	9,146	1,369	495
Total	26,919	4,538	780


a
MAY 23-JULY 10, 1972
CATCH/150 LINE HOURS
No Catch
1-5
6-50
51-100
101-200
201-300
48°
45°
40°
35°
30°
25°
150°
145°
140°
135°
130°
125°
120°
115°


b
MAY 10-JULY 16, 1973
CATCH/150 LINE HOURS
No Catch
1-5
6-50
51-100
101-200
201-300
>301
48°
45°
40°
35°
30°
150°
145°
140°
135°
125°
120°
115°

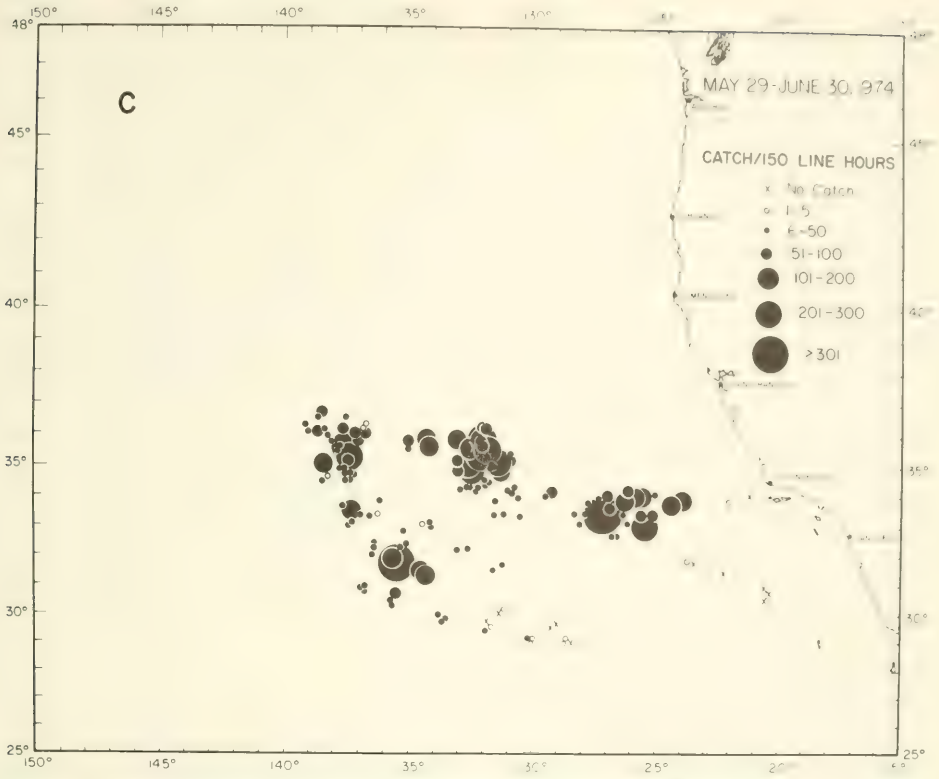
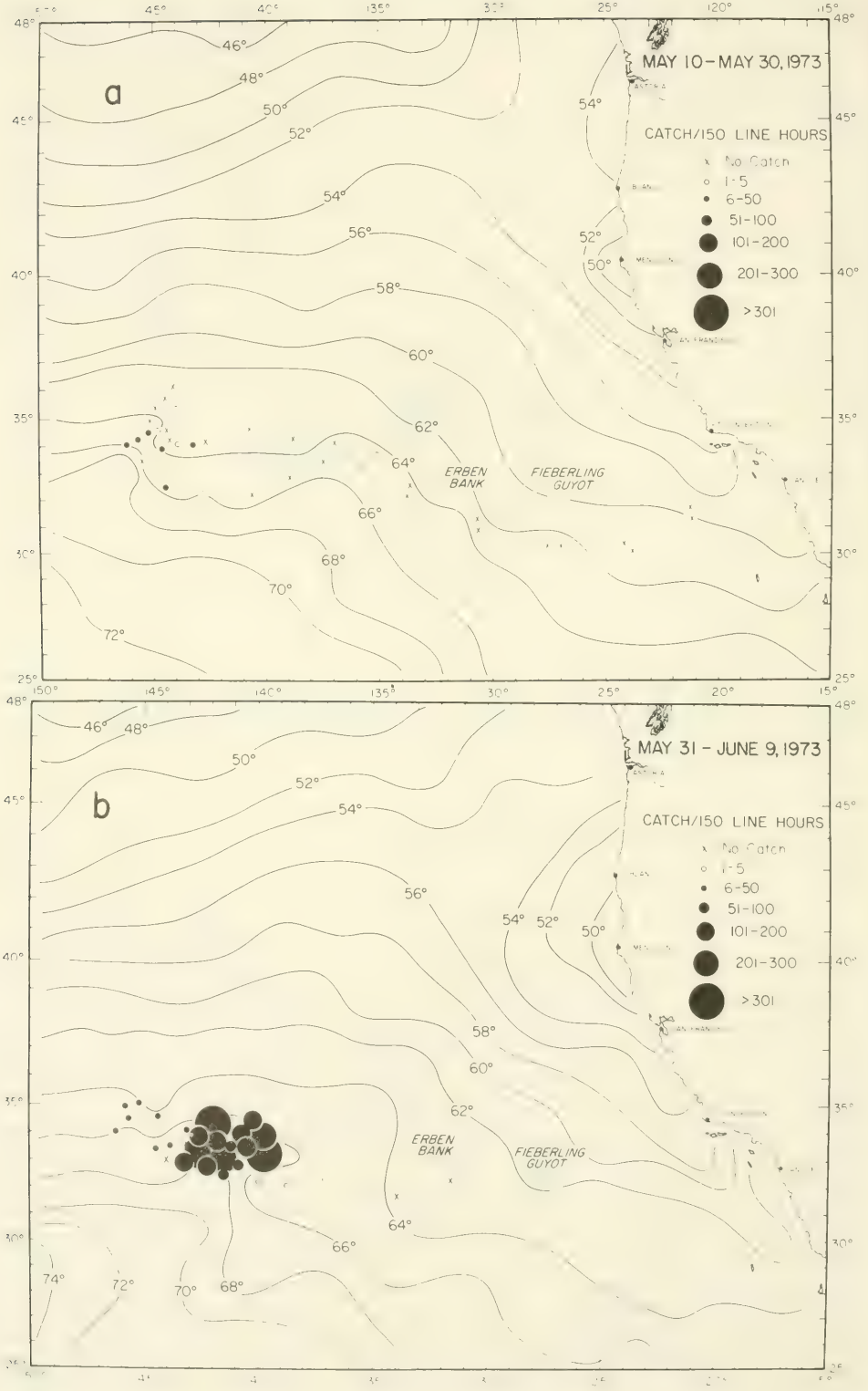


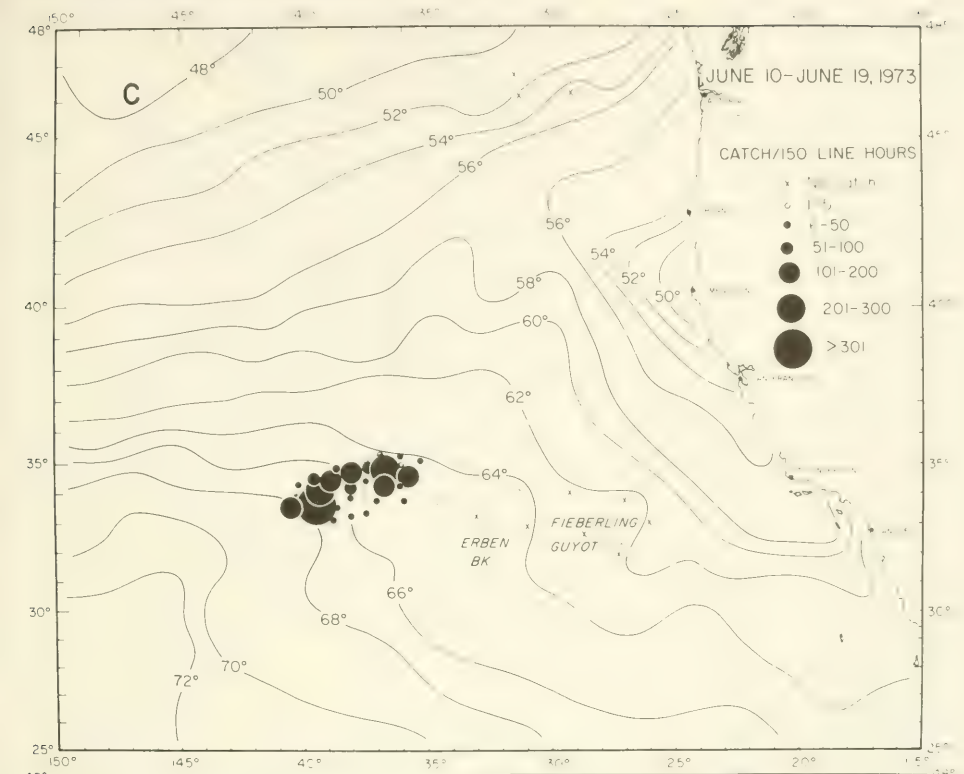
FIGURE 4.—Albacore catch per 150 line-hours by American Fishermen's Research Foundation charter vessels: a. 23 May-10 July 1972; b. 10 May-16 July 1973; c. 29 May-30 June 1974.

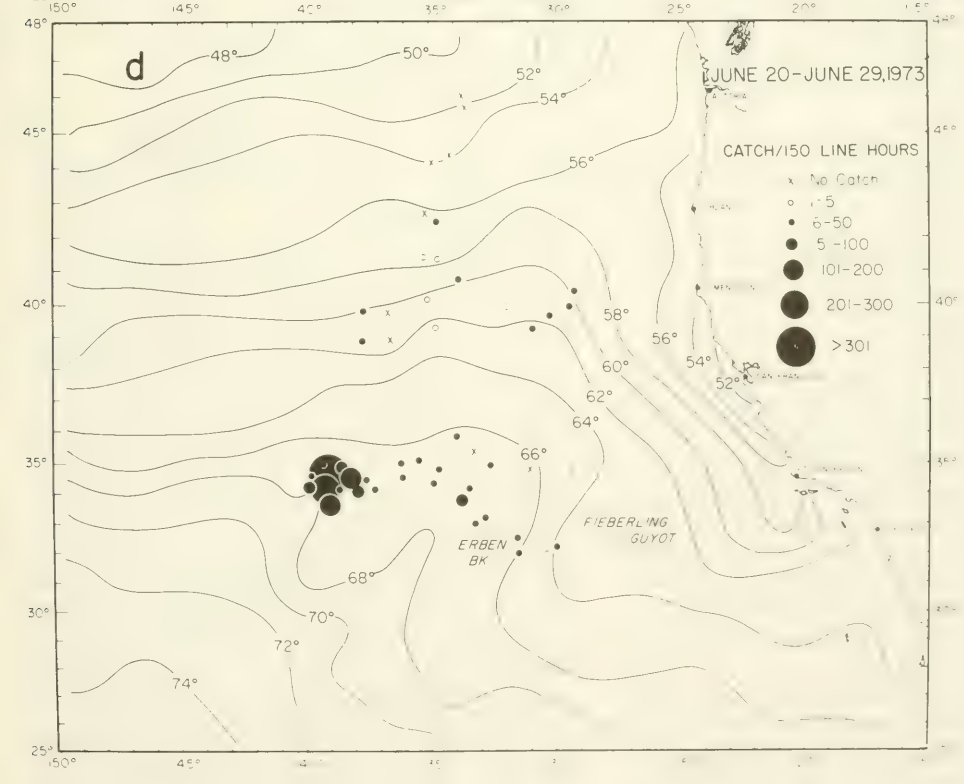
the offshore area of high catches and inshore waters.

Differences Within Surveys

Representative information on spatial and temporal variations in the distribution and relative abundance of albacore in offshore waters during May and June is given in Figure 5a-e. In the early part of the 1973 survey, 10 to 30 May, four vessels worked westward making only small scattered catches between lat. 31° and 35°N, long. 142° and 145°W. In the second time period, 31 May to 9 June, the vessels returned through waters they had scouted earlier and began making catches of over 100 fish/day between lat. 32° and 34°N, long. 139° and 143°W. Good catches continued to be made in the general area of lat. 33° to 35°N, long. 135° to 143°W for several weeks with charter vessels landing up to 300 fish/day on many days. A second group of four charter boats, which left San Diego on 25 May, did not catch any fish until 4 June when they moved westward of long. 139°W near lat. 33° to 35°N. On their return to San Diego during mid-June, the first group of boats failed to catch any fish east of long. 135°W despite favorable ocean temperature conditions. Similarly, on the return to San Diego near the end of June, catches by the second group of charter boats dropped off abruptly east of long. 135°W with only small scattered or no catches made east of Fieberling Guyot (long. 128°W). The four vessels surveying the area north of lat. 38°N found generally poor to moderate catches. (The region lat. 35° to 38°N was not covered by the fishing vessels.) This sequence of catch charts shows that: 1) albacore were apparently unavailable to jig fishing, except for scattered catches, through May in a region which subsequently was to prove very productive; 2) albacore became available to trolling gear in the first week of June in a region which will be shown later to be associated with the subtropic boundary of the Transition Zone; 3) good catches persisted within a block of 2° latitude by 7° longitude for


a
MAY 10–MAY 30, 1973
CATCH/150 LINE HOURS
No Catch
1-5
6-50
51-100
101-200
201-300
>301
ERBEN BANK
FIEBERLING GUYOT
b
MAY 31 – JUNE 9, 1973
CATCH/150 LINE HOURS
No Catch
1-5
6-50
51-100
101-200
201-300
>301
ERBEN BANK
FIEBERLING GUYOT


c
JUNE 10–JUNE 19, 1973
CATCH/150 LINE HOURS
1–50
51–100
101–200
201–300
>301
ERBEN BK
FIEBERLING GUYOT


d
JUNE 20–JUNE 29, 1973
CATCH/150 LINE HOURS
No Catch
1–5
6–50
51–100
101–200
201–300
>301
ERBEN BK
FIEBERLING GUYOT

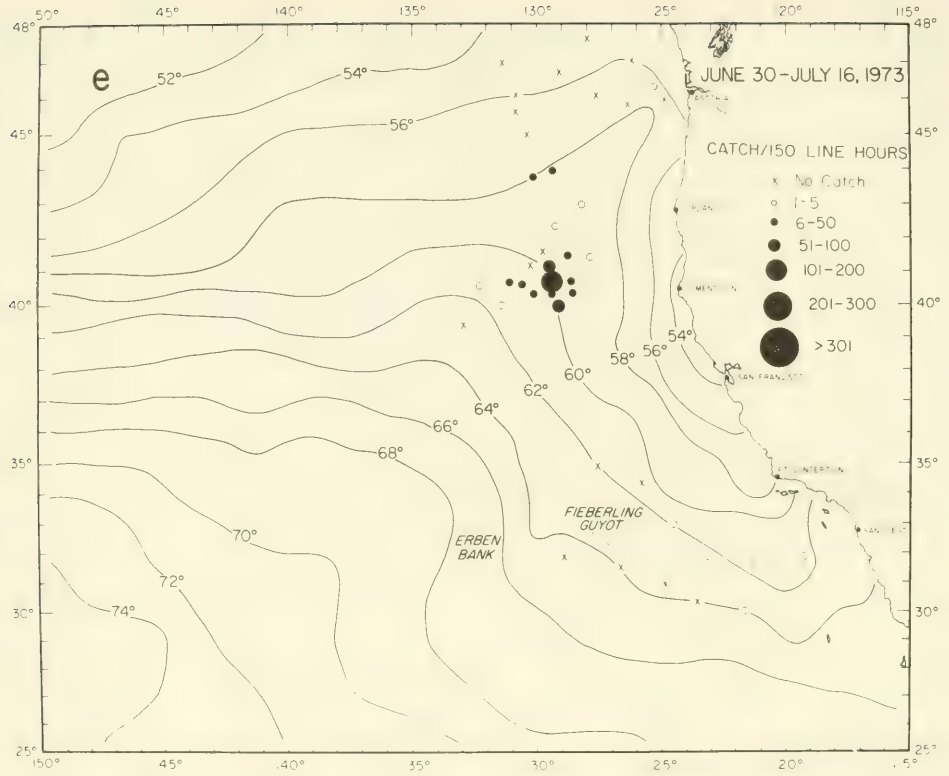


FIGURE 5.—Albacore catch per 150 line-hours by American Fishermen's Research Foundation charter vessels and sea-surface temperature: a. 10-30 May 1973; b. 31 May-9 June 1973; c. 10-19 June 1973; d. 20-29 June 1973; e. 30 June-16 July 1973.

over a 3-wk period in June, and 4) elsewhere catches were substantially lower.

Catches Made By Noncharter Commercial Fishing Vessels

Because of the fishing success of the chartered fishing vessels, in the years following the first survey (1972), noncharter commercial albacore vessels have fished in the offshore region concurrently with the chartered fishing vessels and research vessels. During June 1973 and June 1974 it is estimated that, respectively, 25 to 30 and 50 to 60 albacore vessels fished across a large zone of latitudes in the offshore regions (Jack Bowland pers. commun.). Additional information on the distribution and relative abundance of albacore is provided by these catch data.

Figure 6a-e shows estimates of mean catch-per-unit effort by 15-day period and 1° quadrangle of latitude and longitude for May through July 1973, for those commercial albacore vessels from which logbook records were available. [Logbook records were standardized by methods given in Laurs et al. (1976).]

As with the charter vessels, a center of high relative abundance was found in the offshore region between lat. 33° and 35°N and long. 139° and 143°W. From mid-May through mid-June (Figure 6a, b) no catches were reported north of lat. 36°N nor (with one exception) east of long. 134°W. In the latter half of June (Figure 6c), a scattering of catches was made in the intervening zone. The distribution and relative abundance of albacore, indicated by the charter and noncharter fishing vessel catches, were similar. Catches by noncharter vessels were made over the same latitudinal range and the same offshore to nearshore sequence was observed. The fishing success of the noncharter vessels further demonstrates that commercial concentrations of albacore were available 4 to 6 wk earlier than the normal fishing season in waters hundreds of miles offshore of the area where the fishery has traditionally operated.

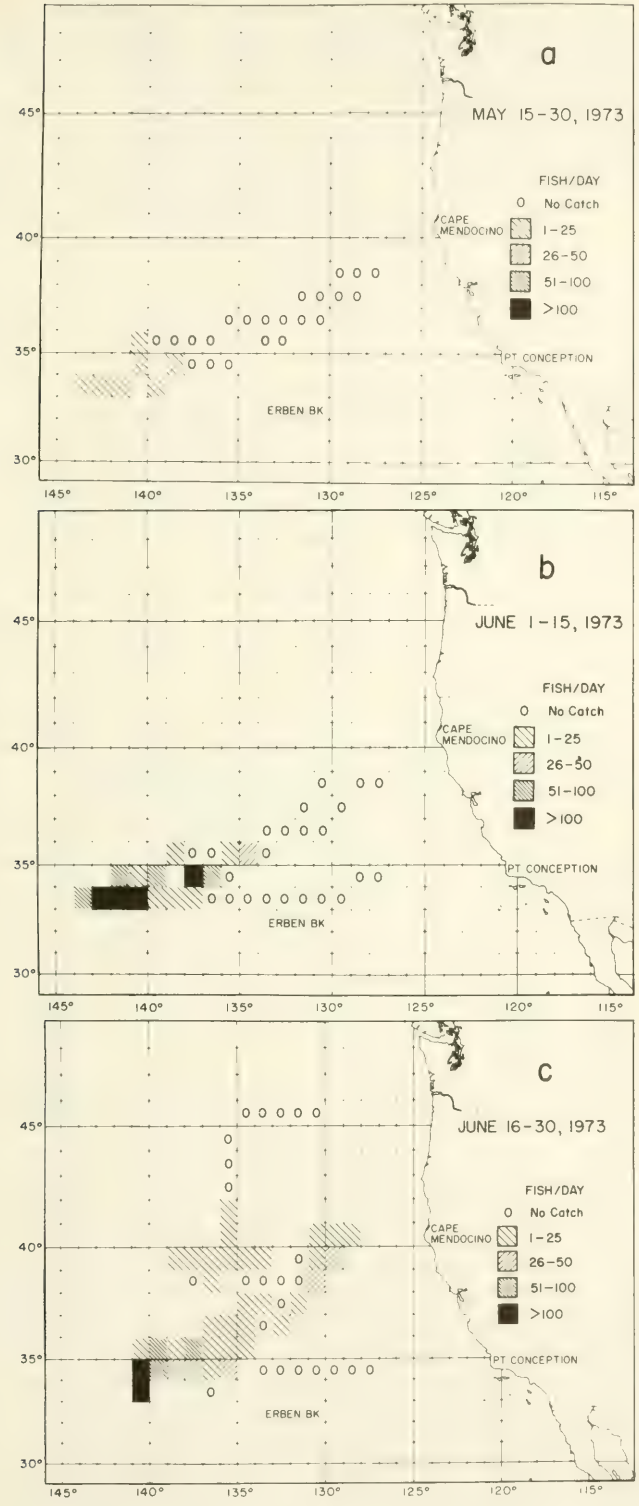


FIGURE 6.—Mean daily albacore catch-per-unit effort by 1° quadrangles for noncharter vessels for the period: a. 16-30 May 1973; b. 1-15 June 1973; c. 16-30 June 1973; d. 1-15 July 1973; e. 16-31 July 1973.

The last two charts in this series (Figure 6d, e, through the end of July 1973) reveal subsequent stages of albacore migration and commencement of the nearshore fishery. The relative abundance of albacore was high in nearshore waters by late July. In comparison to recent years, the 1973 nearshore fishery started about 3 weeks late.

SIZE COMPOSITION OF FISH

Three size modal groups of fish were caught in each year by the AFRF charter vessels; however, the relative proportions of the size groups varied among the years (Figure 7; Table 2). In 1972 about equal proportions of each size modal group were caught. In 1973 and 1974 the medium-size modal group was predominant and the larger one nearly absent.

TABLE 2.—Percentage size composition by number and by weight for albacore catches made by American Fishermen's Research Foundation charter vessels in the offshore area west of long. 130°W and south of lat. 38°N.

Year	<4 kg	4-8 kg	>8 kg	<4 kg	4-8 kg	>8 kg
	Percent by number			*Percent by weight*[1]		
1972	39	33	27	18	33	49
1973	43	53	4	25	65	10
1974	37	61	2	22	73	5

[1]Estimated from length-weight relationship given by Clemens (1961).

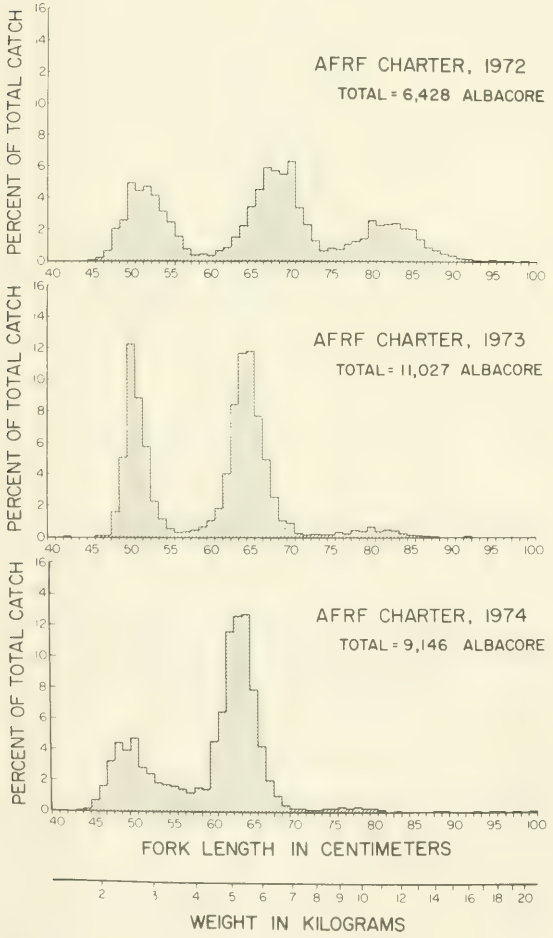


FIGURE 7.—Size composition by percent frequency of catch versus fork length for total catches of albacore from the research surveys in 1972-74.

THE MARINE ENVIRONMENT

Albacore were found mainly in Transition Zone waters. Variations in distribution and relative abundance between each of the surveys appeared to be related to oceanographic conditions of the Transition Zone. Transition Zone waters lie between the cool low salinity Pacific Subarctic waters to the north and the warm, saline Eastern North Pacific Central waters to the south and have temperatures and salinities that are characteristic of a mixture of these two primary water masses (Sverdrup et al. 1942; Christensen and Lee 1965). Transition Zone waters are found in a band across the North Pacific middle latitudes within the North Pacific Current and are bounded by sharp horizontal gradients in temperature and salinity (McGary and Stroup 1956; Roden 1970, 1972, 1975). These bounding gradient regions are sometimes referred to as the Subtropic and Subarctic fronts. The dynamic processes which produce and maintain these gradients also enrich these waters (McGary and Stroup 1956).

An oceanographic section of the vertical distribution of temperature and salinity was taken along long. 137°30′W in June 1972, 1973, and 1974 (Figure 8). In 1972 and 1973, Subarctic waters were found north of lat. 35 °N and Central waters south of lat. 31°30′N and 32°N, respectively. Boundaries of the Transition Zone between these water masses were well developed and readily identifiable. The Subarctic front was marked by abrupt shoaling of the 33.8‰ isohaline and 58°F (14.4°C) isotherm and a sharp horizontal gradient in salinity extending from the surface to greater than 175 m. The Subtropic front was delineated by steep shoaling of the 34.2‰ isohaline and 62°F (16.7°C) isotherm and a sharp gradient in salinity extending from the surface to greater

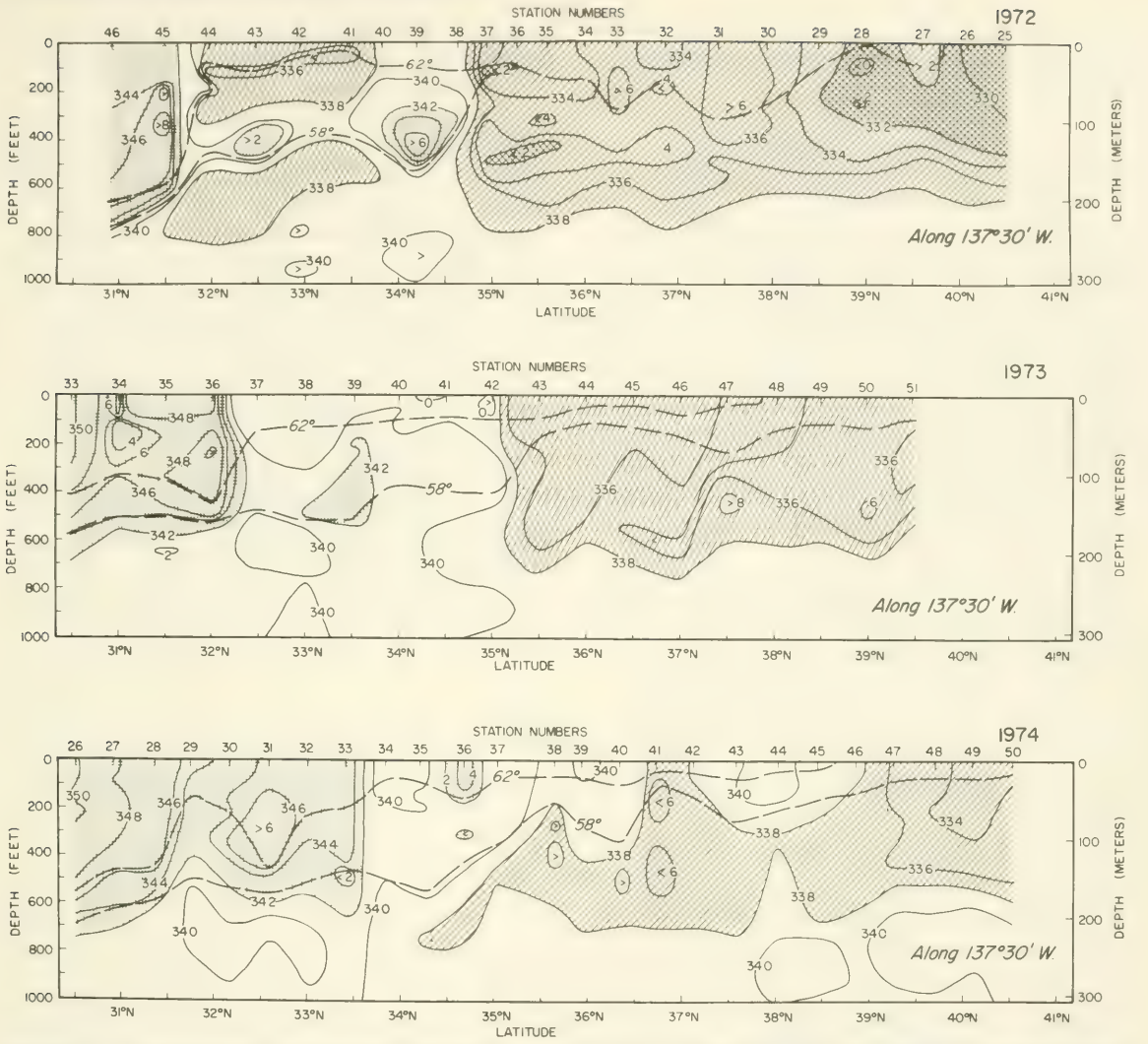


FIGURE 8.—Vertical sections of temperature and salinity along long. 137°30′W during June 1972, 1973, and 1974. Low salinity water (<33.8‰) indicative of Subarctic water is hatched and crosshatched. High salinity water (>34.2‰) indicative of Central water is shaded with a dot pattern. The 58° and 62°F isotherms are shown by heavy dashed lines.

than 150 m. A temperature gradient on the order of 0.6°C in 13 km was often found to mark these fronts at the sea surface. At other times, however, seasonal heating in the surface layer eroded the horizontal temperature gradient at the surface. Mixing was evident in the Transition Zone in 1972 with low-salinity water penetrating southward and some high-salinity water northward at intermediate depths.

Oceanographic conditions were different in the region of the Transition Zone in 1974 from those which were observed in 1972 and 1973. In 1974, boundaries of the Transition Zone were poorly developed and broken. Salinity gradients were diffuse and changes in depth of the isotherms gradual and variable in the regions of the Subarctic and Subtropic fronts. The Subarctic front was virtually nonexistent and Transition Zone waters graded gradually into Subarctic waters. The Subtropic front was weak and spread between lat. 31°30′ and 33°30′N. Saur[8] found that the diffuse

[8]Saur, J. F. T. 1976. Anomalies of surface salinity and temperature on the Honolulu-San Francisco route, June 1966-June 1975. NORPAX Highlights 4:2-4. (Unpubl. rep.)

nature of the Transition Zone and its frontal boundaries became evident late in 1973 and persisted throughout 1974.

ALBACORE CATCHES IN RELATION TO OCEANIC FRONTS

Graphical depictions of the frontal gradients that form the boundaries of the Transition Zone[9] and standardized albacore catches for June of each of the three surveys are shown in Figure 9a-c. This figure indicates that the catches were largely made within the Transition Zone in all 3 yr. During June 1972 and 1973, productive centers of fishing, indicating high relative abundance of albacore, developed in the Transition Zone between lat. 33° and 35°N and west of long. 135°W (Figure 9a, b). These centers persisted for several weeks before fishing effort was ended. In these years, the frontal structure was strongly developed and the Transition Zone easily identifiable. During June 1974 when the frontal structure was poorly developed and water mass boundaries were less distinct, catches were distributed over a larger range of latitude and longitude (Figure 9c). Overall catches in 1974 were substantial but they were not persistent in any area for more than a few days. Thus, while albacore were still associated with Transition Zone waters, the influence of extensive lateral mixing between water masses and the diffuse nature of the boundary frontal structure apparently failed to concentrate fish in a given location for periods of time as had apparently occurred in the previous 2 yr.

While graphical depictions of frontal structure outline the location of the boundaries associated with Transition Zone water (Figure 9a-c), they do not indicate the intensity of the gradients of the frontal structure. The frontal structure has been shown generally to have weak gradients during

[9]The temperature and salinity fields measured by the research vessel, augmented by the XBT data collected by the charter fishing vessels, were analyzed to delineate the frontal gradients.

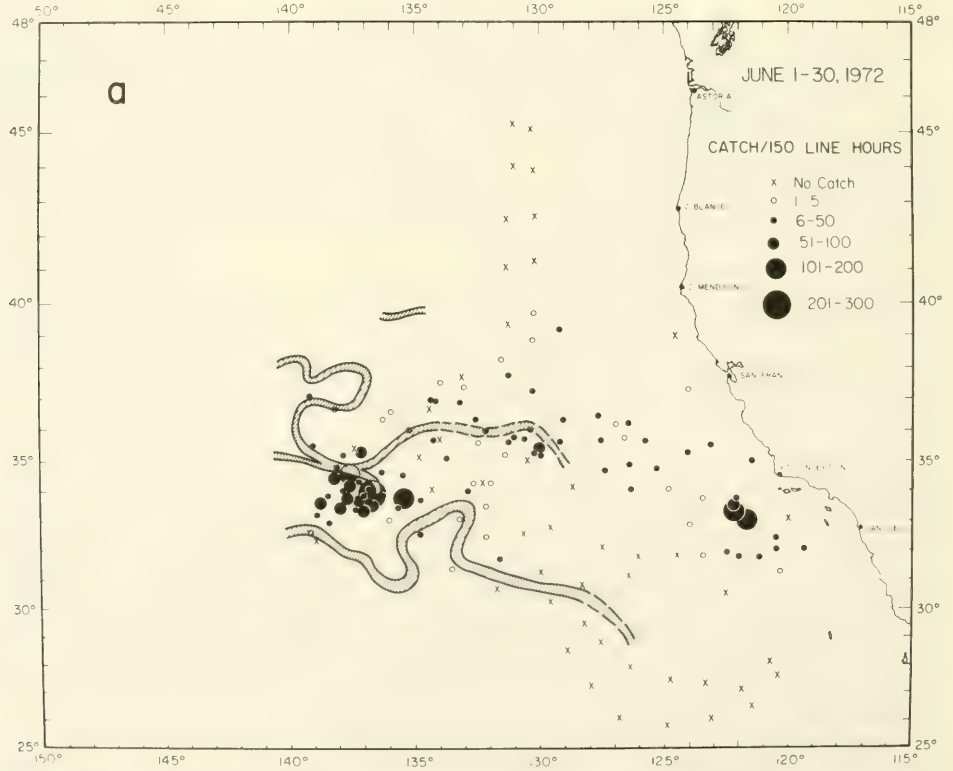
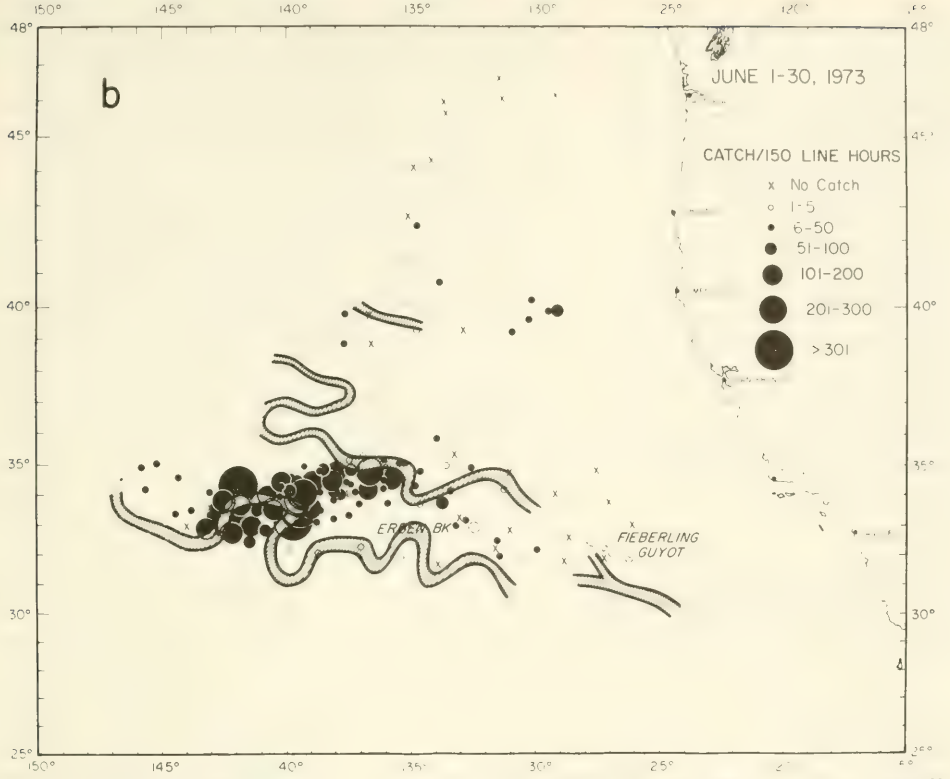
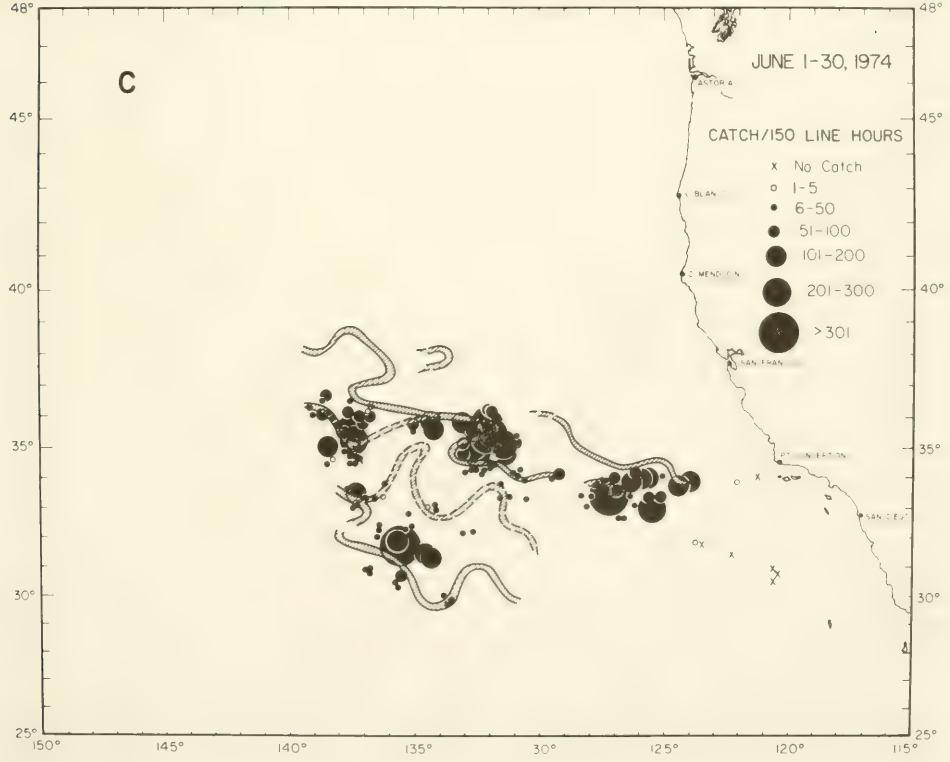


FIGURE 9.—Albacore catch per 150 line-hours by American Fishermen's Research Foundation charter vessels and locations of fronts delineating Transition Zone waters during: a. 1-30 June 1972; b. 1-30 June 1973; c. 1-30 June 1974.


b
JUNE 1-30, 1973
CATCH/150 LINE HOURS
x No Catch
o 1-5
• 6-50
51-100
101-200
201-300
>301
ERBEN BK.
FIEBERLING GUYOT


c
JUNE 1-30, 1974
CATCH/150 LINE HOURS
x No Catch
o 1-5
• 6-50
51-100
101-200
201-300
>301

June 1974; however, one localized area did have sharp, abrupt gradients. The eastward protruding tongue of Transition Zone water centered at lat. 35°30'N, long. 132°30°W had salinity gradients comparable with those found in previous years. Substantial catches of albacore persisted in this one region for a week after which fishing effort was terminated.

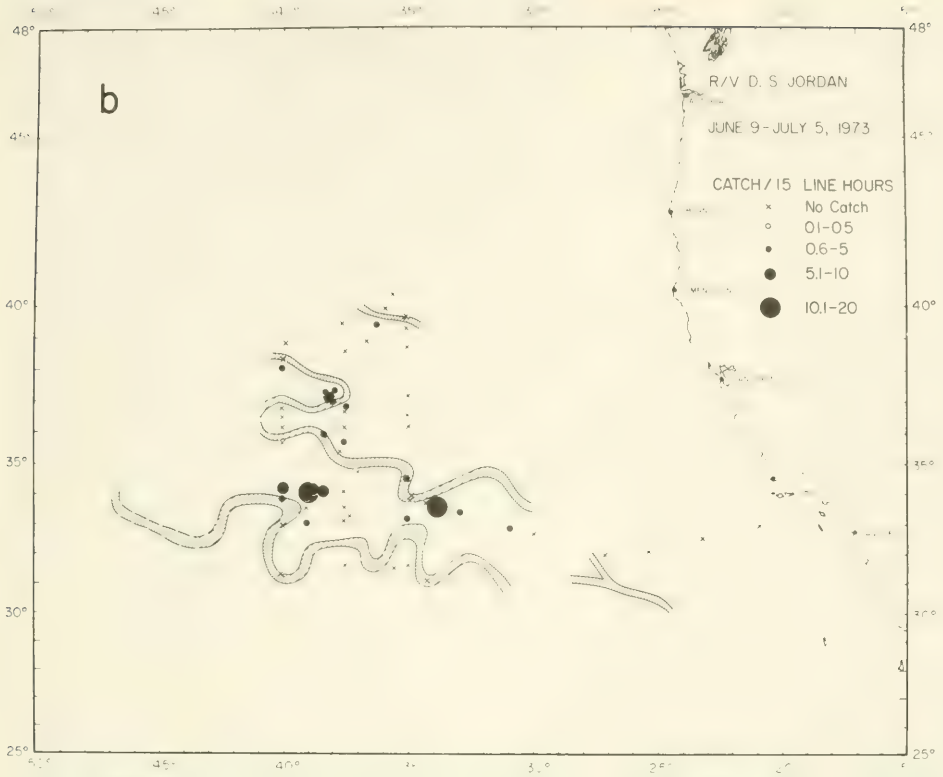
Further information on the distribution of albacore can be derived from the catches made by the research vessels (Figure 10a-c).[10] The research vessels trolled for albacore along tracks that crossed the oceanic fronts and expended fishing effort in Central, Subarctic, and Transition Zone waters. With few exceptions, they did not catch albacore in Central or Subarctic waters. In 1972 and again in 1973, when a large meander developed in the Subarctic front, albacore were taken in the northward protrusion of Transition Zone water (Figure 10a, b). Albacore often were found close to the front. During each of the surveys, catches were made by the research vessel as the frontal gradients were being recorded by shipboard instrumentation.

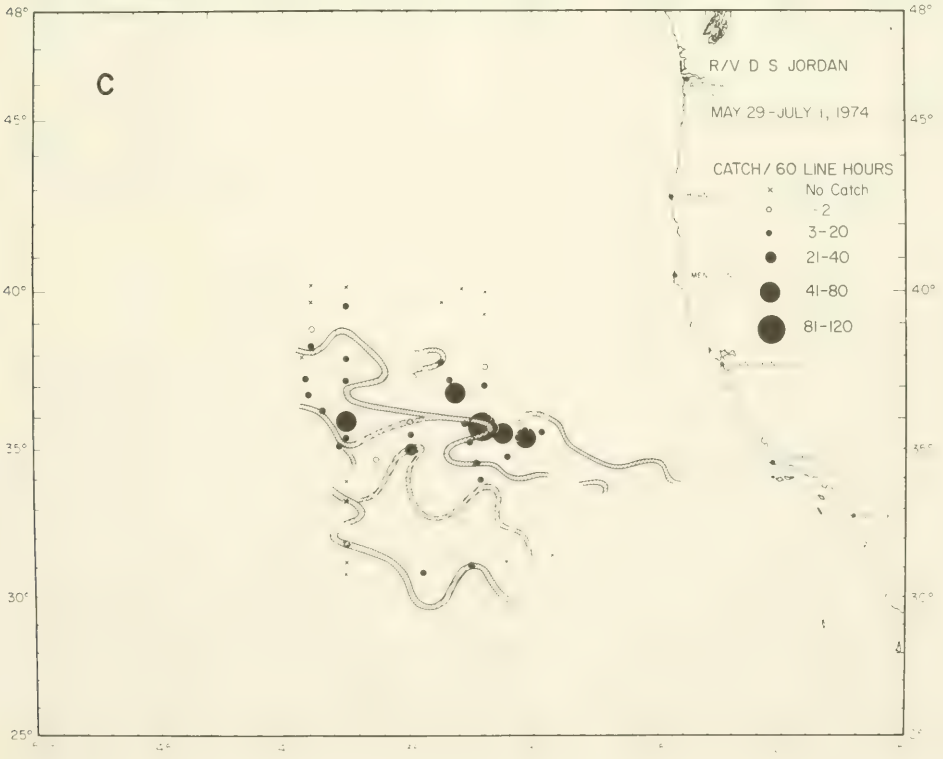
Analyses of variance were performed upon the charter vessel catch data to test the hypothesis that catch rates were dependent upon water mass in the offshore area during June. For the 1972 survey, daily or twice daily XBT casts were matched with the daily catch data. Because specific isotherms were found to fall within very different depth ranges from one water mass to another, the dependence of catch rate upon classes of depth ranges for these isotherms was tested. Thus for this statistical test the water masses may be defined as follows:

Water mass	*Isotherm*	*Depth*
Pacific Subarctic	58°F (14.4°C)	<60 m
Transition Zone	58°F	≥60 m

[10]Catches are expressed in number of fish caught per 15 line-hours in 1972 and 1973 and per 60 line-hours in 1974. These numbers of line-hours approximate the amount of fishing effort expended each day by the research vessels during respective years.

FIGURE 10.—Albacore catch per 15 line-hours by National Marine Fisheries Service research vessel and location of fronts delineating Transition Zone waters during: a. 4-23 June 1972; b. 9 June-5 July 1973; c. 29 May-1 July 1974.


b
R/V D. S. JORDAN
JUNE 9-JULY 5, 1973
CATCH/15 LINE HOURS
No Catch
0.1-0.5
0.6-5
5.1-10
10.1-20
48°
40°
35°
30°
25°


c
R/V D S JORDAN
MAY 29-JULY 1, 1974
CATCH/60 LINE HOURS
No Catch
1-2
3-20
21-40
41-80
81-120
48°
45°
40°
35°
30°
25°

	62°F (16.7°C)	≤90 m
Pacific Central	62°F	>90 m

The data were transformed to logarithms in order to standardize between-sample variance. Results of the analysis of variance show that mean catch in the Transition Zone, which was greatest, is significantly different ($P = 0.01$) from those in other water masses.

For the 1973 survey, both charter and noncharter vessel catches were available for test. The fronts were assumed fixed for this time frame, as shown in Figure 9b, and catches were assigned to a water mass based upon reported geographic position. Because no fishing effort was expended in Central waters, except close to the Subtropic front where catches are expected, an analysis of this division could not be included. Both the charter and noncharter vessel data revealed that mean catches were significantly greater ($P = 0.01$) in the Transition Zone than those in the Subarctic waters.

The poor development of the boundary fronts between water masses during 1974 precludes a definitive assignment of catch to water mass; therefore, a test of the 1974 data was not considered.

Catches made by both the charter fishing vessels and the research vessel during each of the three surveys demonstrate that albacore are distributed within the Transition Zone and may be absent (or unavailable) or nearly so in water masses to the north and south during this phase of their shoreward migration. Relative abundance is high in offshore areas within the Transition Zone waters and at times close to the oceanic fronts that form the boundaries of Transition Zone waters. Further, when the oceanic fronts are diffuse and widely spread there is likely to be a corresponding spread in the distribution of albacore and a dislocation of the centers of high relative abundance.

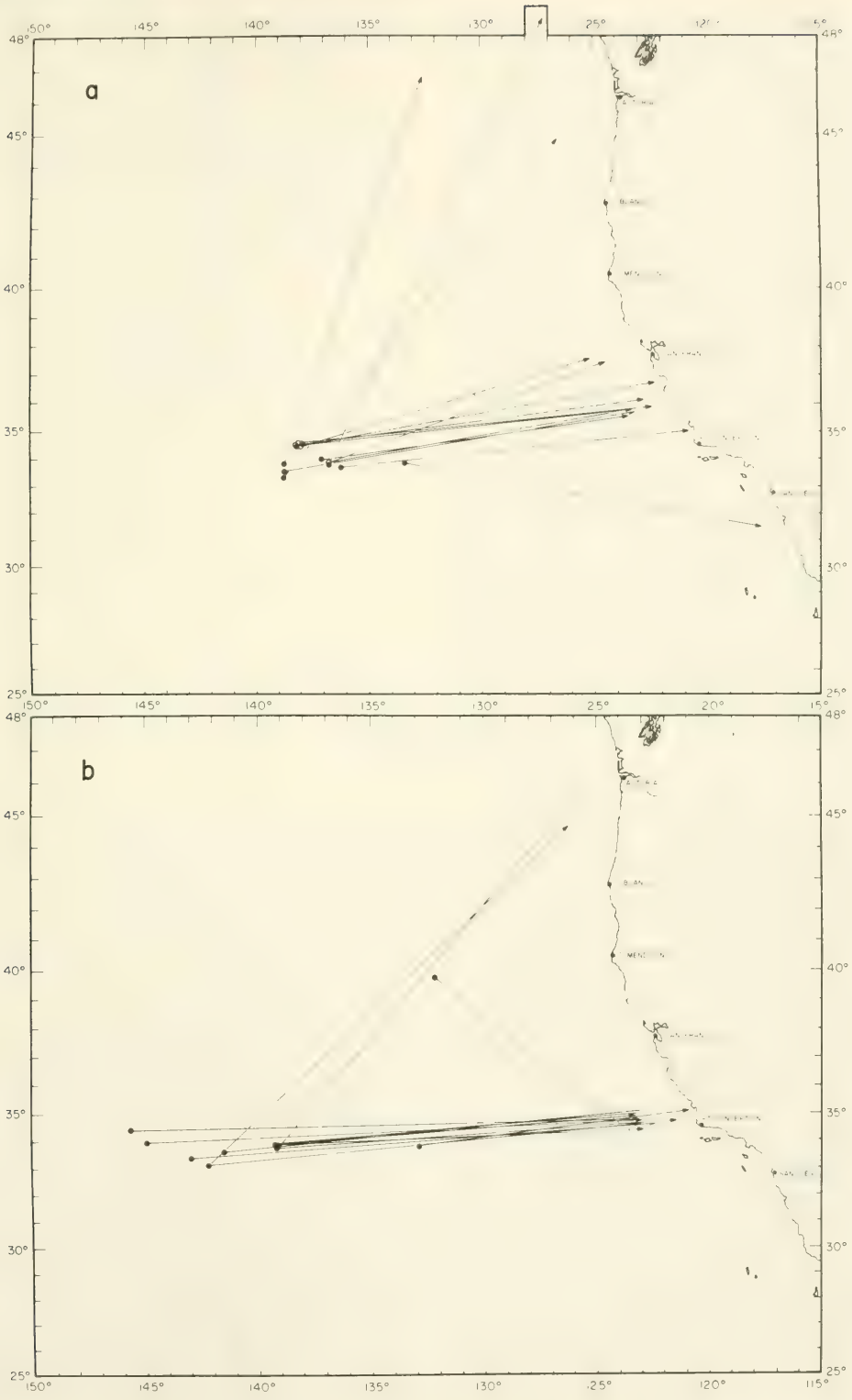
MIGRATION PATTERN FROM OFFSHORE TO NEARSHORE WATERS

We view the general pattern of seasonal migration of albacore into coastal waters where the U.S. fishery traditionally takes place during summer-fall as proceeding in three main stages: First, albacore migrate eastward from central North Pacific regions and form centers of high relative abundance within the eastern sector of the Transition Zone waters 600 to 1,000 mi off the coast. This development initially occurs in late May and June, a time when seasonal warming has raised the surface layer temperature of these waters to values considered to be within the habitat preference for albacore. These concentrations of fish may persist in offshore waters for several weeks. Next, as nearshore waters warm in ensuing weeks, albacore migrate toward coastal regions. Fishing efforts in the intervening zone usually produce only scattered catches, thus suggesting that during the shoreward migration the behavior of the fish is such that they are not available to fishing gear and/or that albacore may not be concentrated. Then, usually by mid-July, concentrations of high relative abundance are found near the coast, often in the vicinity of oceanic fronts related to coastal upwelling. Although variations may occur in this general pattern, the main features of the migration tend to repeat each year. The stages of shoreward migration and initial development of the albacore fishery can be seen in the two series of charts showing nominal catch per unit effort for 1973 (Figures 5a-e, 6a-e).

The shoreward migration of albacore from the central North Pacific into coastal waters appears to continue through the summer months. Albacore trolling experiments conducted from U.S. Navy picket vessels operating approximately between long. 130° and 135°W (Flittner 1963, 1964) showed albacore to be available there throughout the summer. Also, two albacore tagged by the Japanese in the western Pacific (near lat. 35°N and long. 171°E) in mid-June 1974 were recovered in the U.S. fishery in September 1974 (Japanese Fisheries Agency 1975).

Division in Migration Pattern

In order to examine migration of albacore from offshore to nearshore waters, an albacore tagging program was conducted during each of the offshore surveys. Over 4,500 albacore were tagged and released (Table 1). Recoveries of tagged fish made during the same season as released provide information on migration of albacore into nearshore waters (Figure 11a-c). Most recoveries of tagged fish made in 1972 of fish tagged during early season 1972 in waters offshore of long. 130°W were made in central-southern California waters and only a few recoveries were made in Pacific Northwest waters (Figure 11a). A similar recovery pattern was observed in 1973 (Figure 11b). A contrasting recovery pattern was observed in 1974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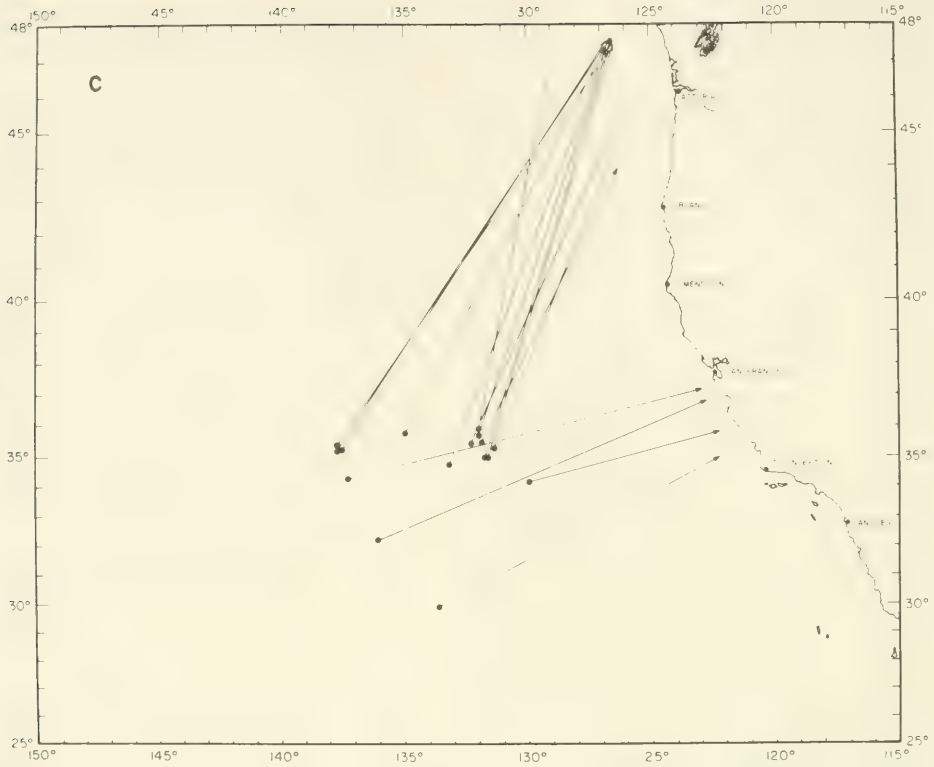

FIGURE 11.—Recoveries made during the same season as release of fish tagged during the early-season surveys in: a. 1972; b. 1973; and c. 1974.

when almost all of the recoveries of fish tagged in 1974 were made in waters off the Pacific Northwest (Figure 11c).

Differences in recovery pattern cannot be accounted for by geographic variations in fishing effort and fish catch. In all 3 yr, 70% or more of the fish caught during the commercial fishery was off the Pacific Northwest. It appears, instead, that differences in recovery patterns could be related to the location where tagged fish were released. In both 1972 and 1973, most of the tagging effort in offshore waters was between lat. 33° and 34°N and in 1974 it was farther north, between lat. 35° and 36°N. The different and divergent patterns apparently are the result of the albacore following different and divergent migration routes toward the nearshore waters. Tagging efforts of 1972 and 1973 and those of 1974 were apparently concentrated upon different branches of the migration. The division in the migration pattern appears to have occurred near lat. 35°N and must have occurred west of, and prior to, the appearance of the fish in the survey region.

Support for this proposed division in the migration pattern of albacore is indicated by differences in length-frequency distribution of albacore caught in the commercial fishery off California and north of California. Differences in size composition of fish caught in 1972 in the two regions (Figure 12 upper and lower) include: 1) the mode of large-size fish was about 5 cm larger in fish caught off California than in fish caught off the Pacific Northwest; 2) the mode of the medium-size fish, which formed the dominant size group in both regions, was 1 to 2 cm larger in fish caught off California than in fish caught off the Pacific Northwest; and 3) occurrence of three modal size groups taken in the fishery off California, but only two off the Pacific Northwest, where the smallest modal size group was absent. Examination of size-frequency distributions for 1973 and 1974 yielded similar results.

The size composition of albacore caught west of long. 130°W by charter vessels in 1972 (Figure 12 lower) was very similar to that for fish taken in the commercial fishery off California (Figure 12 mid-

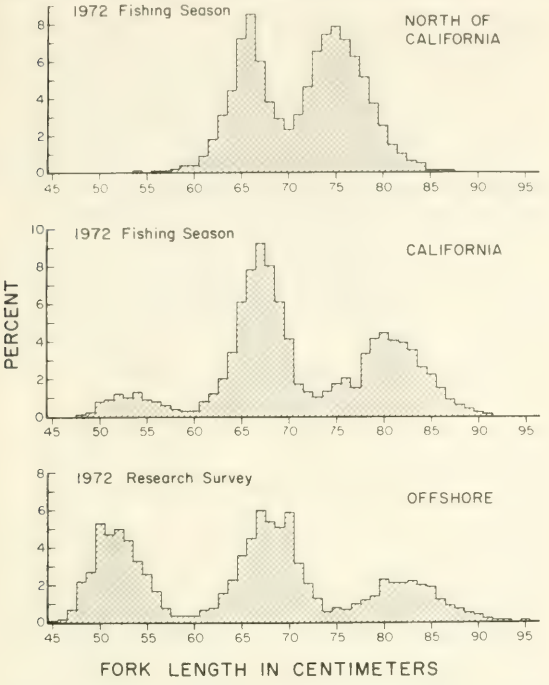

FIGURE 12.—Size composition of albacore caught by U.S. fishermen during 1972 north of California (upper), off California (middle), and size composition of albacore caught during the 1972 National Marine Fisheries Service-American Fishermen's Research Foundation offshore survey (lower).

dle) and hence different from the size composition of fish taken in the commercial fishery north of California (Figure 12 upper). It appears, then, that albacore caught in the offshore region of high relative abundance south of lat. 35°N in 1972 were a part of the migration of fish that reached regions off California.

We interpret the findings concerning offshore-nearshore and north-south geographic variations in size composition as supporting the hypotheses 1) that the fish which compose the fishery off California are separate from those which make up the fishery off the Pacific Northwest, and 2) that these two groups of fish follow different migration routes into nearshore waters.

Movements of Albacore by Size Groups

The size composition data for the 1972 charter vessel catch were stratified into offshore and nearshore regions at long. 130°W and into one 8-day and four 10-day time periods. Graphs of the stratified data standardized by fishing effort for 1972 (Figure 13) show that albacore initially appeared offshore near the end of May and there was an abrupt increase in relative abundance in the beginning of June. A decline in relative abundance was observed offshore after 19 June as centers of abundance shifted to nearshore where there was an increase in early July. Within these overall trends, changes in each of the three modal size groups can be followed. The mid-size modal group (fork length centered about 67 to 69 cm), initially dominated early offshore catches and then diminished in relative importance. It formed almost the entire catch of the first nearshore catches and continued to dominate nearshore catches into July. The large-size modal group (fork length centered about 82 to 85 cm) showed similar trends: a rise and fall in relative abundance offshore and with a subsequent shift to nearshore, but lagging behind the mid-size modal group by one 10-day period. The small-size modal group (fork length centered about 52 and 53 cm) was dominant offshore after 10 June but made little appearance in the nearshore region during the survey. This size group subsequently entered the nearshore fishery, however, as is evident from the size composition of the 1972 fishery off California (Figure 12 middle). An additional geographic division in

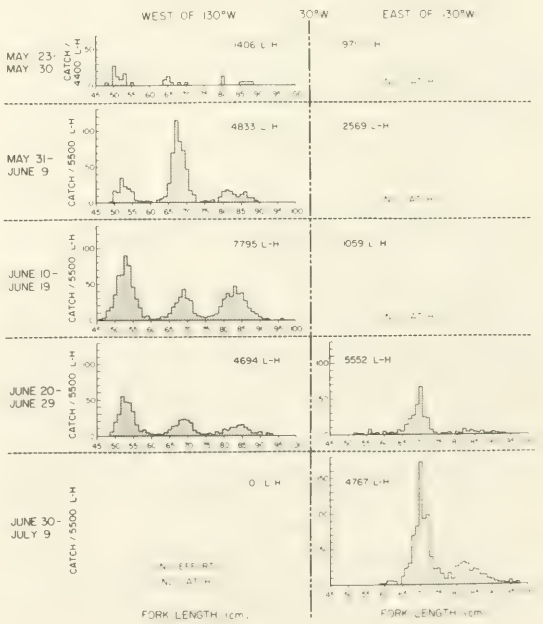

FIGURE 13.—Size composition of albacore caught by American Fishermen's Research Foundation charter vessels in 1972 by time periods and east and west of long. 130°W.

the offshore region, splitting the catch north and south of lat. 35°N showed that the catches first developed south of lat. 35°N and then moved north. By the fourth period (20 to 29 June), the small-size modal group composed almost the entire catch south of lat. 35°N and offshore of long. 135°W.

Several conclusions are evident from these temporal and areal changes in size composition. While catches persisted for up to 4 wk within a 2° by 4° quadrangle of latitude and longitude in the offshore region, changing patterns of size composition suggest that albacore were moving through the region within a period of 10 days or less and that the size groups migrated somewhat independently. The mid-size group, which composes the major portion of the U.S. fishery, led other size groups by 10 or more days. Also, the sequence of compositional changes of each size group and the geographic differences suggest that the migration from the offshore region to the nearshore fishery takes about 20 days or more; at least it did in 1972.

The 1972 catch data were chosen for examination of spatial and temporal changes in size composition because each of the size groups was well represented in the survey catches and all phases of the migration into the fishery are evident, including commencement of the fishery, by the completion of the survey. In 1973 the fishery started late, weeks after the survey, and in 1974 the patterns were less distinct, apparently in response to weak oceanic frontal conditions.

DISCUSSION

Association of Albacore Distribution With Oceanic Frontal Regions

The commercial fisheries on North Pacific albacore and the migration of albacore among these fisheries have frequently been associated with oceanic frontal regions in the western Pacific (Yamanaka et al. 1969; Uda 1973; other works), in the central North Pacific (Shomura and Otsu 1956; McGary et al. 1961), and in coastal upwelling regions (Pearcy and Mueller 1970; Panshin 1971; Laurs 1973; Laurs et al. 1977).

Results of our study provide evidence for the continuity of the association of albacore distribution with the Transition Zone and frontal boundaries into the eastern North Pacific. Catches made by the AFRF charter fishing vessels and the research vessel during each of the three surveys demonstrate that albacore are distributed mainly within the Transition Zone and usually are absent (or unavailable) in water masses to the north and south. Furthermore, our work strengthens the general concept that the distribution and relative abundance of large, highly migratory fish may be markedly influenced by oceanic frontal features. Other studies usually have had to rely on mean ocean conditions and/or statistically averaged fishery data, whereas our fishery and oceanographic data were collected concurrently during several surveys, and the amounts of fishing effort, fish catch, and oceanographic data were substantial.

Relative Abundance of Albacore in the Eastern Sector of the Transition Zone

We have found centers of high relative abundance of albacore in June within the eastern sector of the Transition Zone and often close to its frontal boundaries. Annual and intra-annual areal variations in relative abundance of albacore were observed and appeared to be related to development of the frontal boundaries of the Transition Zone. When the Subarctic and Subtropic fronts were strongly developed, areas of high relative abundance developed within relatively narrow bands in the Transition Zone and persisted for several weeks. When the Transition Zone was broader and the fronts were poorly developed, centers of high relative abundance were found over a larger area within the Transition Zone and did not persist for more than several days in any one location.

Based on scouting results from several research surveys, it appears that the timing and the location of fishing effort may be critical in locating centers of high relative abundance of fish in the eastern sector of the Transition Zone. In 1973, charter vessels first found a center of high relative abundance on 4 June near lat. 34°N, long. 140°W in Transition Zone waters. For several weeks prior to this finding, the AFRF charter vessels had made only scattered catches while scouting in and about this same area. Thus, it seems that the center of high relative abundance appeared in a surge within the first week of June. In 1955, an albacore survey cruise by a single U.S. Bureau of Commercial Fisheries (BCF) research vessel *(Hugh M. Smith)* scouted this area in late May and early June (Graham 1957). Seven longline sets and trolling conducted between lat. 41° and 28°N along long. 139°W resulted in only a single albacore

being taken before the vessel departed the area on 5 June. The 1955 scouting effort may have been too early by a matter of days to weeks to locate substantial numbers of fish. In 1957, a BCF fishery research vessel *(John R. Manning)* scouted to the north and east of this area in late June (Callaway and McGary 1959). Small to modest catches of albacore were made by trolling and in gill net sets in and about the Transition Zone, but the area which we have found to have a center of high relative abundance was not scouted.

Extension in Space and Time of U.S. Albacore Fishery

The cooperative NMFS-AFRF albacore research surveys have demonstrated the feasibility of extending the U.S. fishery for albacore in space and time. Albacore were caught by chartered fishing vessels in commercial concentrations considerably farther offshore than where the albacore fishery has traditionally taken place and up to 6 wk prior to the usual beginning of the fishing season. Noncharter commercial albacore fishing vessels, attracted to the early season offshore fishery by the research survey findings, have begun operating in this fishery in increasing numbers.

While fishing results of the AFRF-chartered and the nonchartered fishing vessels indicate that commercial amounts of fish can be caught earlier and farther offshore than the usual fishing season, additional experience is needed to examine the variability of this extension of the fishery, especially in terms of timing and availability, in order to judge properly whether it can provide a dependable contribution to the U.S. fishery. If in the long-run the early season offshore fishery proves viable, its development could be an important factor in reducing annual fluctuations in the catch of albacore. According to Clemens (1962) large annual fluctuations in catch are a prominent feature of the U.S. albacore fishery. Stabilization of catch among years could contribute significantly to the proper utilization and ultimately to the effective management of the resource.

The fishing success by charter and noncharter albacore commercial fishing vessels in 1972-74 is in contrast to an earlier attempt to establish commercial fishing in waters offshore from where the U.S. fishery has historically operated. According to McGary et al. (1961), an unsuccessful gill net and trolling effort was made in the summer of 1958 by a chartered commercial fishing vessel in areas of the central North Pacific where albacore were caught during research surveys conducted in summers of 1955 and 1956. The failure to catch albacore in amounts sufficient to support commercial fishing may have been an accidental event related to intense anomalous oceanic conditions which occurred ocean-wide and affected numerous fisheries in 1957-58 (Sette and Isaacs 1960).

Association of Shoreward Albacore Migration With Transition Zone and Possible Mechanisms

Shoreward Migration and Transition Zone

Based on association of albacore distribution and relative abundance with the Transition Zone and its frontal boundaries, we conclude that the shoreward migration of albacore is linked to the Transition Zone and that variations in the pattern of migration occur in response to variations in the character and development of the Transition Zone and its frontal structure. When the Transition Zone is narrow and its fronts are well developed, as in 1972 and 1973, the migration pattern of the fish is narrow and relatively well defined. In contrast, when the Transition Zone is broad and its fronts weakly formed, as in 1974, the migration pattern of fish is wide and less well defined.

There is also some suggestion that the strength and continuity of the Transition Zone fronts in offshore waters may affect the timing of arrival of fish in nearshore waters. When the fronts are well developed, fish appear to aggregate in their vicinity, resulting in a tendency for the fish to remain in offshore waters for periods of time that delay their arrival in the nearshore fishing grounds. However, when the fronts are weak the fish appear to move through offshore waters with less delay and arrive earlier in nearshore waters. Initial showing of fish in nearshore waters during the years of the surveys supports this speculation. The nearshore commercial fishery and sport fishery off southern California commenced several weeks later in 1972 and 1973 than in 1974.

Possible Mechanisms for Association of Albacore With the Transition Zone

The mechanisms responsible for the relationship between albacore and the Transition Zone and its frontal boundaries may result from a

number of factors acting in an interrelated matrix which impacts the fish both directly through physiological means and indirectly through forage availability. We postulate that the factors include, but are probably not limited to: 1) habitat temperature preference, 2) biological productivity, and 3) thermal gradients as they affect the albacore's thermoregulation processes, and that these factors act in an interrelated way superimposed on the innate drive of the fish to migrate across the North Pacific Ocean.

HABITAT TEMPERATURE PREFERENCE. — The distribution and relative abundance of albacore are related to sea-surface temperature (Clemens 1961; Johnson 1962; Panshin 1971; and others). The habitat temperature preference for albacore ranges from approximately 16° to 19°C (Clemens 1961; Laveastu and Hela 1970). This temperature range is found in the upper mixed layer waters of the Transition Zone in spring. Near-surface waters to the south of the Transition Zone are generally warmer than this and those to the north cooler.

The sequence of spring-summer warming of the surface layer along a section between Honolulu and San Francisco during 1972 is illustrated in Figure 14. The Transition Zone boundaries identified by the abrupt changes in depth of isotherms at intermediate depths fall between long. 130° and 140° W. The habitat temperature preference range for albacore (16° to 19°C) is shown with shading. In early and mid-spring (upper left) only the Central waters have preferred temperatures and these waters occur down to a considerable depth, almost 200 m. In subsequent time periods, a shallow sur-

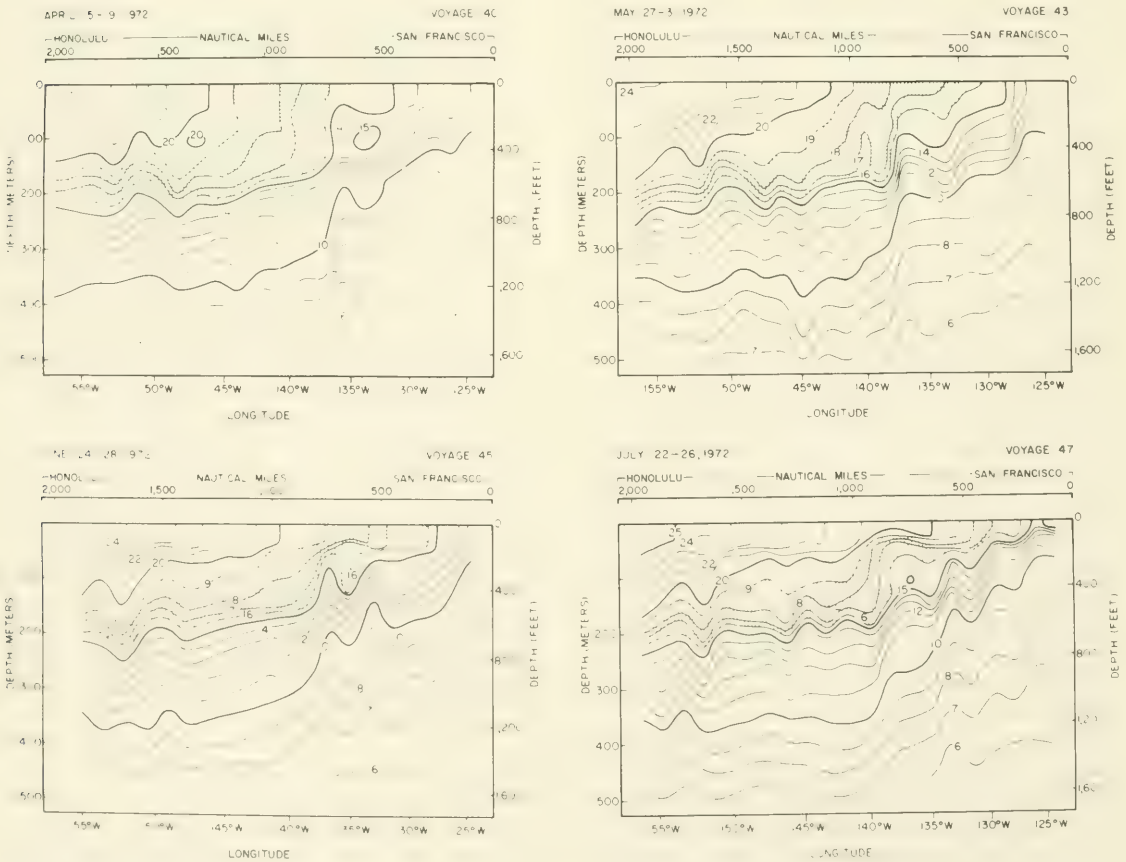

FIGURE 14.— Vertical temperature sections on a transect from Honolulu to San Francisco during April to July 1972. The temperature range between 16° and 19°C (60.8° and 66.2°F) is shaded.

face layer develops and warms to preferred temperatures, initially in the Transition Zone and then in more nearshore waters. It is near the end of May and through June that the preferred temperature range occurs in the Transition Zone and is generally restricted to depths <70 m. The depth limitation of preferred waters greatly improves the vulnerability of albacore to surface trolling gear.

BIOLOGICAL PRODUCTIVITY.—Tagging data show that migration of albacore from the western to the eastern North Pacific is active with an average migration speed of 48 km/day for 78- and 80-cm fish (Japanese Fisheries Agency 1975). This suggests that an albacore requires considerable energy to complete the transpacific migration. Sharp and Dotson (1977) calculated that the caloric expenditure per hour for a swimming albacore 63 cm in fork length is 5.02 kcal/h. They also speculated that fat stores may be an important energy source utilized by albacore for migration. Studies of the food habits of albacore caught during the surveys[11] show that albacore feed actively in offshore waters during their shoreward migration. The composition of the food found in the stomachs is different from that of fish caught in inshore waters (Pinkas et al. 1971, Laurs and Nishimoto MS[12]), but average volumes of food in stomachs from the two regions are similar. Therefore, availability of forage is likely to be an important factor influencing the route of albacore migration.

There are three major oceanic habitats in the North Pacific which are separated by pronounced latitudinal faunal boundaries and steep latitudinal gradients in standing stocks of phytoplankton and zooplankton (McGowan and Williams 1973). These species and biomass boundaries are coincident with the boundaries of the Pacific Subarctic, Transition Zone, and Pacific Central waters (Johnson and Brinton 1963). A northward increasing step-cline occurs among the North Pacific habitats in standing stocks of phytoplankton (Venrick et al. 1973; McGowan and Williams 1973), zooplankton (Reid 1962; McGowan and Williams 1973), and micronekton (Aron 1962), and in primary production (Koblents-Mishke 1965). Zooplankton and micronekton standing stock estimates made during the offshore albacore surveys show similar results with values generally being highest in Subarctic waters, intermediate in Transition Zone waters, and lowest in Central waters.

Since biological productivity is higher in Subarctic waters than in Transition Zone or Central waters, it would be most advantageous from the standpoint of food availability for albacore to confine their migration path to Subarctic waters. However, during spring months the temperature of the Subarctic waters is much lower than the habitat preference for albacore. We conclude, then, that the northern limit of the albacore migration route during spring is determined by ocean temperature and that the limiting temperature is found near the northern boundary of the Transition Zone. The temperature of the upper layer of the Central waters is higher than the habitat temperature preference for albacore, but there are temperatures below the upper layer which lie within the habitat temperature preference for albacore. Thus, temperature could restrict the distribution of albacore from the upper layer but not at some depth interval below the upper layer. We propose that while temperature may play a role in determining the southern limit of the albacore distribution and migration route, the major factor is the abundance and availability of forage organisms which drop off sharply near the southern boundary of the Transition Zone.

OCEAN THERMAL GRADIENTS AND THERMOREGULATION OF ALBACORE.—Thermoregulation processes by albacore may be an important factor in determining their association with the Transition Zone and its frontal boundaries. Thermoregulation is characteristic of tunas and certain other fishes (Carey et al. 1971). According to Neill (1976) for fishes as a group, the only effective means of regulating body temperature is by behavioral regulation of the immediate environmental temperature through locomotory movements.

Computer simulation models developed by Neill (1976) indicate that where environmental conditions are characterized by large expanses of isothermal or nearly isothermal water separated by relatively narrow thermal discontinuities (e.g., oceanic frontal systems), fishes will be relatively concentrated near the discontinuities.

[11]Laurs, R. M., and R. N. Nishimoto. 1973. Food habits of albacore caught in offshore area. *In* Report of joint National Marine Fisheries Service-American Fishermen's Research Foundation albacore studies conducted during 1973, p. 36-40. (Unpubl. rep.)

[12]Laurs, R. M., and R. N. Nishimoto. Food habits of albacore in the eastern North Pacific. (Unpubl. manuscr.)

Division in the Migration of Albacore Into the American Fishery

Our study indicates that there is a division in the migration pattern of albacore into the American fishery with fish which compose the fishery off the Pacific Northwest and off California following different routes. We believe that the "northern" branch of the migration progresses as described by Powell et al. (1952) who, during an exploratory albacore fishing survey over a region off the Pacific Northwest, found albacore along a warm-water edge that develops seasonally 400 to 500 n.mi. offshore of southern Oregon in late June and early July. The warmwater edge was observed to progress northward and coastward in a bulge or pouchlike pattern as seasonal warming of the surface waters took place over the ensuing weeks. The occurrence of albacore was found to follow the progression of the warmwater zone shoreward and northward along the coasts of Oregon and Washington and by mid-August to waters off the Queen Charlotte Islands, British Columbia. Powell et al. (1952) concluded that these findings, as well as earlier observations, indicated that the main barrier directly or indirectly influencing the distribution of albacore throughout their northern range is water temperature.

Clemens (1961) investigated the onset and movements of the albacore fishery off California and Baja California for the fishing seasons 1951 through 1953. From catch records he found that albacore entered the coastal waters as far south as 200 n.mi. south of Guadalupe Island (lat. 29°N) in some years and as far north as the San Juan Seamount (lat. 33°N) in others. He also presented tag recovery data which showed that albacore move from Baja California or southern California in the early season northward to central California as the season progresses (however, only one recovery of a tagged fish was made off northern California). Clemens concluded that albacore entering the American fishery initially migrate to Baja California or southern California and that longshore movement was the dominant mode of their dispersal into coastal zones to the north. Although he allowed that albacore may reach Oregon and Washington waters by following the seasonal bulge of warm offshore water as suggested by Powell et al. (1952), Clemens stated that a large part of the main body of albacore travel northward up the coast to waters off the Pacific Northwest from Baja California and southern California. No evidence was given for this statement and our newer findings do not support it. We concur that northward longshore movement is important in nearshore waters, but conclude that fish entering waters off Baja California or southern California do not migrate farther north than about San Francisco before leaving the American fishery.

Flittner (1963) presented a schematic diagram of albacore movement off the Pacific coast based on albacore catches made by U.S. Navy picket vessels during 1960-62. The picket vessels, stationed 200 to 500 n.mi. offshore (no farther west than long. 135°W) and spaced at latitudinal intervals of 300 n.mi., each trolled several jig lines from May through October. Flittner said that albacore appeared to congregate within an "optimum-temperature" zone and seem to split into two migratory components. Early arrivals proceed to southern feeding areas and late arrivals turn to the northern area, each movement depending upon the progression of seasonal warming.

Progression of seasonal warming continues to appear to be an important factor affecting paths of albacore migration. However, influence of the Transition Zone development and the division of migration pattern described here add considerable complexity to earlier ideas. Our findings suggest that events in offshore waters are important in determining the distribution and relative abundance of albacore in coastal waters.

Pacific Northwest and California Groups of Fish

Based on offshore-nearshore and north-south geographic variations in size composition of albacore we postulate that the group of fish which compose the albacore fishery off California are separate from those which make up the fishery off the Pacific Northwest. Brock (1943) arrived at a similar conclusion after comparing length-frequency distributions of albacore landed in San Pedro, Calif., and Astoria, Oreg. Brock found differences in size composition and stated, "This would argue that the schools of fish off the Oregon coast were not a part of the schools appearing off the California coast, even though, as indicated above, the two groups may have had a common origin. . . The time of arrival of fish and their abundance as shown by the monthly commercial catch for the ports discussed here (San Pedro and Astoria) make it seem likely that at least two separate groups of schools invaded the coastal

area, one in the north off Oregon and the other in the south off southern California."

Results of studies on the artificial radionuclide ^{60}Co in albacore provide additional evidence that the "northern" and "southern" groups of fish are independent. Krygier and Pearcy (1977) found that the peak activity levels of ^{60}Co in albacore off Oregon occurred a year earlier than the peak activity levels seen by Hodge et al. (1973) off southern California. According to Krygier and Pearcy, the heaviest fallout input of ^{60}Co into the North Pacific occurred at about lat. 40°N. They speculated that due to circulation in the North Pacific, albacore which were associated with waters north of lat. 35°N could have experienced high levels of ^{60}Co up to a year before the tuna associated with waters to the south. They concluded that, "Circulation in the North Pacific and the latitudinal differences in the location of the two portions of the albacore population [as proposed by Laurs and Lynn in this paper] appear to be a plausible explanation for the difference of 1 yr in activity peaks between albacore caught off Oregon by us and those off southern and Baja California by Hodge et al. (1973)." Thus, strong evidence from several independent sources points toward two separate groups of albacore following separate migration paths.

ACKNOWLEDGMENTS

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BIOLOGY OF THE SUMMER FLOUNDER, *PARALICHTHYS DENTATUS*, IN DELAWARE BAY[1]

RONAL W. SMITH AND FRANKLIN C. DAIBER[2]

ABSTRACT

Data on the age, growth, food habits, and racial characters of summer flounder, *Paralichthys dentatus*, from Delaware Bay were examined. Fish were present year-round, although 95% were taken from May through September, and no mature fish were caught during the winter. Fish were aged from annuli on the largest left otolith. The growth rate for males was described by $L_{t+1} = 141.91 + 0.767(L_t)$, and for females $L_{t+1} = 136.72 + 0.843(L_t)$. The Delaware Bay commercial fishery in 1966 was primarily supported by age-groups 2 through 5. The total length-weight relationship was described by, log weight (grams) = log 0.404×10^{-5} + 3.151 log [total length (millimeters)], and the total length-standard length relationship by, total length (millimeters) = 16.695 + 1.55[standard length (millimeters)]. Age and sex made no significant difference in meristic character evaluation. The reported range of variation for some characters was extended: dorsal rays, 89-98; anal rays, 63-78; pectoral rays, 10-13; vertebrae, 40-43; standard length/head length, 3.64-4.30; and head length/upper jaw length, 1.54-2.26.

One objective of this study was to investigate the age, growth, and food habits of summer flounder, *Paralichthys dentatus* (Linnaeus), caught in Delaware Bay. Previous research on age and growth, Eldridge (1962) and Poole (1961), disagreed and additional study was needed.

A second objective was to determine the magnitude of variation in meristic characters of summer flounder from Delaware Bay for comparison with other geographic areas. Ginsburg (1952) reported that summer flounder from Chesapeake Bay and from Beaufort, N.C., might belong to two distinct racial stocks on the basis of gill raker frequency distributions. According to Poole (1966), unpublished studies found no real differences between these populations, but he added that analysis of racial data from Maryland, Virginia, and North Carolina areas suggested the need for additional research.

Summer flounder are common from Cape Cod to North Carolina and they have been reported from Maine to Texas (Bigelow and Schroeder 1953; Poole 1962). They normally inhabit coastal and estuarine waters during the warmer months of the year and move off on the continental shelf in 20 to 100 fm of water during the fall and winter (Bigelow and Schroeder 1953). Spawning occurs during the fall and winter while the fish are moving offshore or at their wintering location, and larvae and postlarvae drift and migrate inshore to coastal and estuarine nursery areas (Smith 1973).

COLLECTION OF MATERIAL

Most fish examined were caught by a 9-m (30-ft) otter trawl, 7.6-cm (3-in) stretch mesh in the body and 5.1 cm (2 in) in the cod end, during monthly fish survey trips in Delaware Bay. A total of 13 sectors were sampled during the period August 1966 through November 1971 (Figure 1), with a minimum of 3 and a maximum of 12 sampled in any 1-mo interval. Sectors sampled were selected to cover a range of salinities and depths in Delaware Bay. During the summer of 1968, three sectors were sampled during the day and again that night. Sampling at each station consisted of making a Nansen cast within 2 m of the bottom for temperature and a water sample, and trawling for 30 min. The mean tow length was 1.2 n.mi. Average water depth for each tow was determined by eye from a recording fathometer trace. Some fish were taken by beach seining, while others were caught during miscellaneous trawling operations through February 1973.

Stomachs for gut analysis were removed immediately on fish capture and placed in 95% isopropyl alcohol.

The commercial summer flounder catch from

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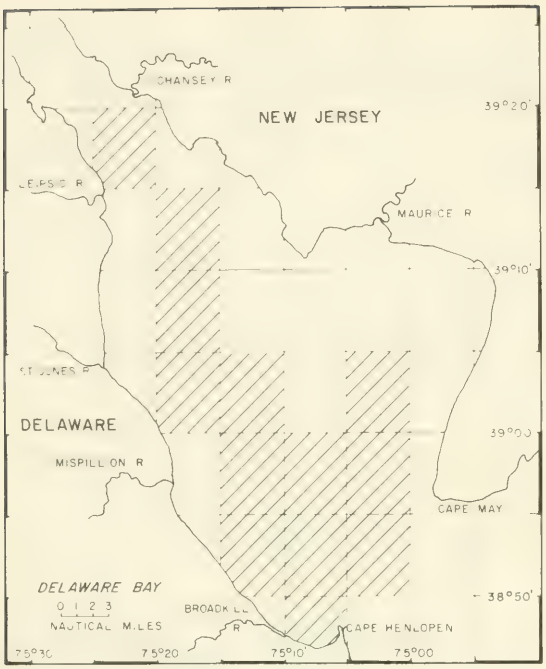

FIGURE 1.—Delaware Bay with sampling sectors shaded.

Delaware Bay was sampled on four occasions in 1966 by measuring all (1,060) fish caught by a 14-m trawler using both a 15-m (50-ft) otter trawl, body—7.6-cm (3-in) stretch mesh, cod end—5.1 cm (2 in), and a 16-m (52-ft) otter trawl, body—10.2 cm (4 in), cod end—7.6 cm (3 in). This vessel was typical of the few commercial boats operating in the bay then, and 1966 was the last year trawling was permitted.

GENERAL OBSERVATIONS

Summer flounder seem to have a ubiquitous range in Delaware Bay. They were caught in all sectors sampled; and in water with temperatures from 1.6° to 26.8°C, salinities from 10.6 to 31.8‰, and depths from the shore to 25 m. Most (95%) fish were caught from May through September. A few juvenile fish were taken in every winter month, indicating that some juveniles move to deeper parts of the estuary during the winter rather than offshore. Poole (1966) suggested a similar phenomenon for estuaries in North Carolina.

During the 5-yr survey, the yearly mean number of summer flounder caught per nautical mile of trawling (number of fish caught per year divided by the total length of tows containing summer flounder) varied from 1.5 to 4.7, with no significant trend. No real difference was apparent in the number (34 day versus 29 night) of flounder caught between day and night tows.

AGE AND GROWTH ANALYSIS

Otoliths were used for aging fish because they were much easier to read than scales, and both Poole (1961) and Eldridge (1962) found them suitable for aging. Left and right otoliths were examined, and we found the radial length (distance from the center of the core to the anterior tip) was different between left and right ones from the same fish. This occurred because the center area or core (Figure 2) was located more posteriorly in the right otolith. We did not compare left and right otoliths to see if the relationship between radial length and the various annuli lengths were the same for both.

Left otoliths were removed from all flounder (either fresh or previously frozen) caught in

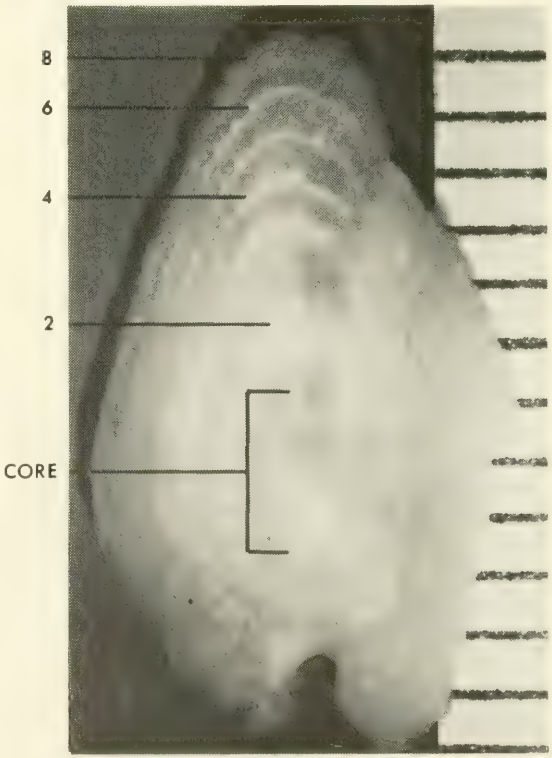

FIGURE 2.—Left otolith from an age-group 8 summer flounder, total length 69 cm, with estimated age indicated against respective annuli (rule marking in millimeters).

1966-68. Upon removal, they were cleaned in water and stored dry. Prior to examination, otoliths were soaked for 30 min in a 2% solution of the plant enzyme, papain, according to the technique of Pruter and Alverson (1962) for cleaning and clearing. Annuli were visible before soaking and it is doubtful this clearing process helped.

For examination, otoliths were placed in distilled water in the wells of a Coor's[3] black porcelain spot plate. They were measured with an ocular micrometer to the nearest 0.1 mm for radial length and annuli lengths with the concave surface up. All otoliths were read twice, and those very difficult to interpret a third time. Approximately 20% of the otoliths were discarded because of irregular shape or indistinct annuli, leaving 319 used in the age analysis. Mean annuli lengths are given in Table 1. No age-group 6 males were collected in this study.

There was a linear relationship between total length (TL in millimeters) and otolith radial length in millimeters, and this relationship was best described by:

$$\text{Otolith radial length} = 0.012(\text{TL})$$

$$\text{Correlation coefficient} = 0.998$$
$$\text{Standard error of estimate} = 0.336$$

This equation applied to both sexes.

Fish length at time of annulus formation or back-calculated length was calculated as described in Rounsefell and Everhart (1953), and these lengths for males and females are given in Tables 2 and 3, respectively. No correction factor was used in the calculation because: 1) the line best representing the total length-otolith radial length relationship had a zero origin and 2) correction factors obtained were not reasonable because they gave the fish a negative length at time of otolith formation. According to Rugh (1962), who used *Fundulus heteroclitus* as an example of a typical teleost, otoliths start to form in the first quarter of development. Therefore, fish length at time of otolith first formation could be considered negligible when compared with fish length at 1 yr.

The observed 17 cm length at 1 yr as reported by Eldridge (1962) is far above a 12 cm length we back-calculated using the otolith core edge as the first annulus. We assumed the first annulus was located at the core edge (radial length from 1.1 to 1.5 mm) because typically the first well-defined annulus away from the core (approximately 3.3 mm radial length, Table 1) was only present in otoliths from fish larger than 27 cm, fish we believed too large to be in age-group 1 (fish 1 or 1+ yr old). Supporting our belief is Eldridge's reported length frequency at 1 yr and our subsequent capture (1973) of Delaware Bay flounder during winter in the 15-20 cm size range. A few otoliths we examined had faint rings at radial lengths of 2.0 to 2.6 mm, but we thought these represented a false annulus. Probably these faint rings were true first annuli and they were not observed in most otoliths.

The primary reason for the difference between our back-calculated fish lengths and those given by Poole (1961) and Eldridge (1962), Tables 2 and 3, is the interpretation of age at the first annulus used. Examination of Poole's calculated length at 1 yr plus his photographs of otoliths indicated he considered the first well-defined annulus as being

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Mean radial distance ± 1 standard deviation of annuli on otoliths from summer flounder taken in Delaware Bay during 1966-68. (No suitable first annulus was found.)

Age-group	Number of otoliths	Measured radial distance for successive annuli (mm)						
		2	3	4	5	6	7	8
Male:								
2	44	3.3±0.3						
3	51	3.2±0.3	4.2±0.3					
4	23	3.2±0.3	4.2±0.3	4.9±0.2				
5	11	3.2±0.2	4.2±0.2	4.9±0.3	5.4±0.3			
7	1	3.0	4.3	4.8	5.6	6.1	6.4	
Female:								
2	50	3.4±0.2						
3	71	3.4±0.2	4.6±0.3					
4	36	3.3±0.3	4.6±0.3	5.5±0.3				
5	22	3.3±0.3	4.6±0.4	5.4±0.4	6.0±0.4			
6	4	3.4±0.1	4.7±0.2	5.6±0.3	6.4±0.4	7.1±0.4		
7	3	3.2±0.1	4.3±0.6	5.3±0.5	6.2±0.4	7.1±0.7	7.9±0.8	
8	3	3.2±0.3	4.3±0.5	5.1±0.4	5.7±0.5	6.3±0.6	6.8±0.6	7.2±0.6

TABLE 2.—Mean back-calculated total length ± 1 standard deviation and annual percent increase in mean total length for male summer flounder captured in Delaware Bay during 1966-68. Included for comparison are mean back-calculated lengths from other studies.

Age-group	Number of fish	Back-calculated length at successive annuli (mm)							
		1	2	3	4	5	6	7	8
2	44		277 ±20						
3	51		261 ±23	344 ±16					
4	23		258 ±21	342 ±17	400 ±14				
5	11		261 ±12	348 ±10	403 ± 9	445 ±11			
7	1		242	347	388	452	493	517	
Mean length			260	345	397	448	493	517	
Annual % increase			24.6	13.1	11.4	9.1	4.6		
Poole (1961)		251	326	387	427				
Eldridge (1962)[1]		170	240	319	357	381	399	414	426

[1]Lengths given for Eldridge at the end of year 1 and 2 are estimates of the average observed length frequency.

TABLE 3.—Mean back-calculated total length ± 1 standard deviation and annual percent increase in mean total length for female summer flounder captured in Delaware Bay during 1966-68. Included for comparison are mean back-calculated lengths from other studies.

Age-group	Number of fish	Back-calculated length at successive annuli (mm)								
		1	2	3	4	5	6	7	8	9
2	50		301 ±21							
3	71		280 ±19	383 ±21						
4	36		279 ±25	389 ±24	465 ±25					
5	22		289 ±20	399 ±24	470 ±22	526 ±22				
6	4		273 ±23	379 ±33	450 ±21	512 ±22	568 ±25			
7	3		252 ±12	332 ±48	412 ±34	484 ± 5	553 ±16	612 ±19		
8	3		289 ±12	395 ±20	469 ± 6	521 ±12	575 ±18	624 ±14	661 ± 9	
Mean length			280	380	453	511	565	618	661	
Annual % increase			26.3	16.1	11.4	9.6	8.6	6.5		
Poole (1961)		271	377	465	531	644				
Eldridge (1962)[1]		170	240	377	424	471	518	566	613	657

[1]Lengths given for Eldridge at the end of year 1 and 2 are estimates of the average observed length frequency.

formed at the end of the first year. Eldridge decided that Poole's calculated length at 1 yr seemed too high when compared with observed length frequencies, so he considered this first well-defined annulus to be formed at first spawning, or at the end of the flounder's third year. We considered the first well-defined annulus to be formed at age 2. Therefore, Poole's age 1 fish = our age 2 fish = Eldridge's age 3 fish. Work by Richards (1970) supported our age interpretation. He found summer flounder growth curves generated by analog simulation only fit Poole's length data when Poole's age-groups were shifted 1 yr forward, i.e., his age 1 fish were made age 2. Richards did not examine Eldridge's age data.

Comparing Poole's (1961) lengths to ours after adjustment for age interpretation, we find them similar except for age 5 females. With age interpretation adjustment, Eldridge's (1962) lengths for males are smaller than ours except at ages 2 and 3 when they are larger, and his lengths for females are noticeable larger until age 5 when they begin to agree quite well.

The length-frequency distribution of the 1966 commercial catch and the 1966-71 research catch revealed that both were primarily composed of age-groups 2 through 5. Figure 3, using the 1966 and 1968 research catch because lengths were by sex, is representative of this distribution. This age composition is similar to the age composition reported by Poole (1961) for the sport fishery catch of Great South Bay, N.Y., after adjustment is made for age interpretation differences.

Equations representing growth rates from Walford's growth transformation (Rounsefell and Everhart 1953) are:

$$\text{for males} \quad L_{t+1} = 141.91 + 0.767\,(L_t)$$

$$\text{Correlation coefficient} = 0.996$$
$$\text{Standard error of estimate} = 7.39$$

$$\text{for females} \quad L_{t+1} = 136.72 + 0.843(L_t)$$

$$\text{Correlation coefficient} = 0.998$$
$$\text{Standard error of estimate} = 6.20$$

where L_{t+1} = fish length (millimeters) at time t plus 1 yr

L_t = fish length (millimeters) at time t.

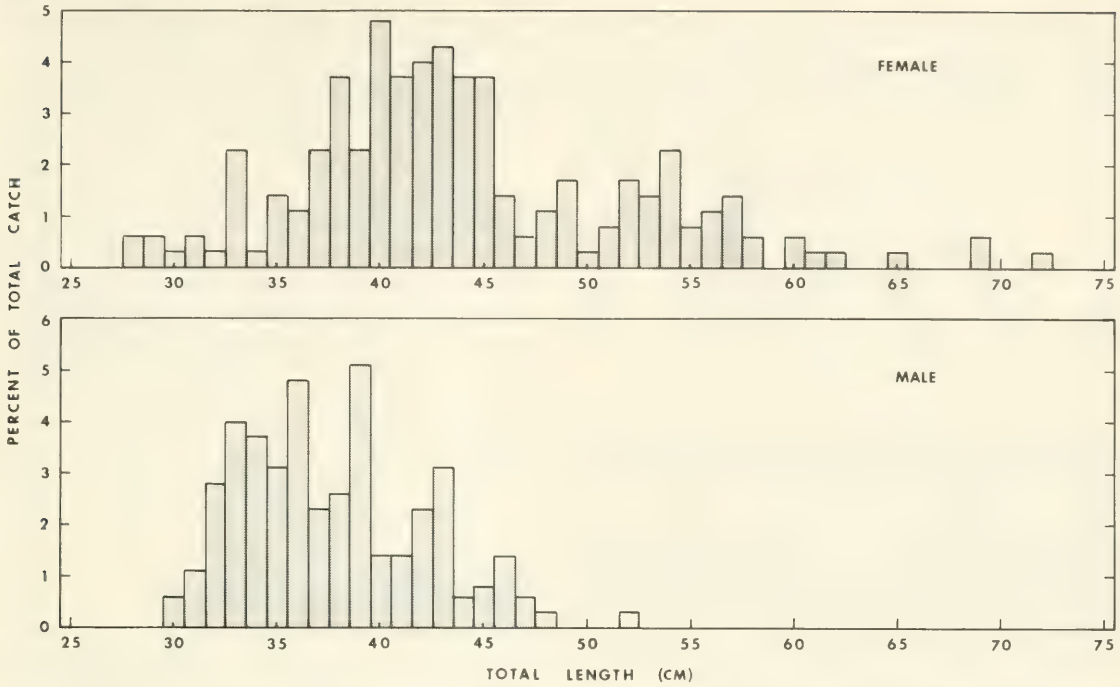

FIGURE 3.—Total length-frequency distribution for 149 male and 202 female summer flounder caught in Delaware Bay in 1966 and 1968.

We found no significant difference in growth rates between the sexes, although both Poole (1961) and Eldridge (1962) did report a significant difference. The growth rates probably are significantly different, an indication of this being the large difference in predicted maximum lengths from Walford's growth transformation (62 cm for males and 88 cm for females), but our limited sample size in older age-groups, particularly males, prevented this difference from being significant. The percent increase in annual length (Tables 2, 3) is similar for both sexes until age 6, and then it begins to decline more rapidly in males.

Our calculated growth rates underestimate those actually observed. Bigelow and Schroeder (1953) stated that the largest summer flounder for which they could find a definite record weighed 11,793 g (26 lb), and the largest fish recorded in sport fishing was 94 cm (37 in) long and weighed 9,072 g (20 lb). Using our predicted maximum lengths and length-weight relationship (see next section), we calculated that a male 62 cm (24.4 in) would weigh 2,339 g (5.21 lb) and a female 88 cm (34.7 in) would weigh 8,199 g (18.1 lb). Also our predicted length of 14 cm at age 1 (Y-axis intercept from Walford's growth transformation) is 3 cm smaller than the observed length given by Eldridge (1962). The lack of samples from age-group 1 and above age-group 8 and the limited samples in age-groups 6 through 8 might account for most of this error. A small change in the female growth rate would give a predicted maximum length of 98 cm, and then we have a fish weighing 11,793 g (26 lb). The growth rate of fish in age-groups 2 through 5 may approximate the growth of the same age-groups in the actual population.

LENGTH AND WEIGHT RELATIONSHIPS

A linear relationship existed between total length-standard length (Table 4), standard length-head length, and head length-upper jaw length. There were no significant differences in these relationships when the sexes are considered separately. The slope (3.151) of the line representing the total length-weight relationship (Table 4) was not significantly different from that (3.146) reported by Lux and Porter (1966) for summer flounder caught in June off Massachusetts. They found no difference between the slopes of the lines when sex was considered, but

TABLE 4.—Calculated values for regression equations describing the total length (TL in millimeters)-weight (W in grams) relationship and the total length (TL in millimeters)-standard length (SL in millimeters) relationship for summer flounder from Delaware Bay.

Number of fish	Sex	Intercept	Slope	Correlation coefficient	Standard error of estimate
		log W = log intercept + slope (log TL)			
[1]333	both	0.404×10^{-5}	3.151	0.995	0.095
102	male	0.102×10^{-4}	2.994	0.953	0.086
167	female	0.227×10^{-5}	3.246	0.987	0.086
		TL = intercept + slope (SL)			
314	both	16.695	1.155	0.986	4.035
102	male	11.044	1.173	0.994	3.531
168	female	18.861	1.150	0.998	4.351

[1]This includes 20 juveniles from North Carolina.

they stated that males were slightly heavier than females on an equal length basis. We found no real difference between the weights of equal sized males and females in Delaware Bay, nor did Eldridge (1962) for fish off Virginia. Twenty fish from North Carolina were included in our total length-weight relationship so we could have some data points from fish in age-groups 0 and 1.

GONAD DEVELOPMENT

Summer flounder gonads were examined from 1966 to 1968 for size and the ovaries for the presence of eggs. Gonads were small and flaccid from April through mid-August. From mid-August through November, the gonads began to enlarge or mature, and the ovaries contained eggs up to 0.4 mm in diameter. Murawski[4] stated that the size of mature eggs is 1.0 to 1.1 mm. There was never more than one-third of any catch during the fall with ripening gonads, and no mature fish were caught from December through March. We concluded that fish leave the bay as they ripen, supporting reports that summer flounder spawn after moving offshore during the winter. The smallest male taken with ripening testes was 30.5 cm, and the smallest female with ripening ovaries was 36 cm. These observations agree with those reported by Eldridge (1962) who stated summer flounder become sexually mature at age 3.

FOOD PREFERENCE

Stomachs from 131 flounder, ranging in size from 31 to 72.5 cm, were examined under a dissecting microscope, and 57% of them contained food. Food items found, listed in order of percent frequency of occurrence were: sand shrimp (*Crangon septemspinosa*, 41%), weakfish (*Cynoscion regalis*, 33%), mysid (*Neomysis americana*, 20%), anchovy (*Anchoa* sp., 7%), squid (*Loligo* sp., 4%), silverside (*Menidia menidia*, 1%), herring (*Alosa* sp., 1%), hermit crab (*Pagurus longicarpus*, 1%), and isopod (*Olencira praegustator*, 1%). On a volume basis weakfish were first, sand shrimp second, and the rest remained in the same order. Fish under 45 cm fed predominantly on invertebrates, while larger ones ate more fish. Poole (1964) found sand shrimp the primary organism eaten by summer flounder in Great South Bay, and that out of 10 fish species eaten, the winter flounder, *Pseudopleuronectes americanus*, was first by weight and the weakfish next to last. These observations indicate that the diet of summer flounder reflects local abundances of prey species.

Flounder caught during the day had a greater volume of food in their stomachs ($\bar{x}$ = 5.1 ml) than those caught at night ($\bar{x}$ = 3.3 ml), but the difference was not significant according to t-tests.

RACIAL ANALYSIS

The following morphometric and meristic characters were measured or counted on fish caught in 1966: total, standard, head, and upper jaw lengths; dorsal, anal, and pectoral fin rays; gill rakers on the first arch; and vertebrae (Table 5). All measurements and counts were made on the left side for uniformity. The number of caudal fin rays (17) and pyloric caeca (4) was constant so counting of these characters stopped after 20 fish. Woolcott et al. (1968) reported 18 caudal fin rays, with the posteriormost dorsal ray being very small and easily overlooked in unstained specimens. We missed this 18th ray in our count.

Ranges of some meristic and morphometric characters examined exceed those reported in the literature (Table 5). Analysis of variance showed no significant difference in the counts of the six variable meristic characters due to age or sex.

Comparison by t-test of meristic character counts on summer flounder sampled in Delaware Bay, Chesapeake Bay, and North Carolina (Table 6) gave inconclusive results. There was no significant difference between these areas for numbers of dorsal fin rays and vertebrae. Differences based on gill raker counts by Woolcott et al. (1968) might not be valid, because Deubler (1958) stated

[4]Murawski, W. S. 1966. Fluke investigations. N.J. Fed. Aid Proj. F-15-R-7 (Completion Rep. Job No. 3). N.J. Dep. Conserv. Econ. Dev., 24 p.

TABLE 5.—Meristic and morphometric data for summer flounder taken from Delaware Bay in 1966, and ranges reported in the literature that were exceeded.

Characters	Number of fish	Range	Mean	Standard error	Literature reported range
Meristic:					
Dorsal fin rays	194	80-98	88.92	0.20	[1]80-96
Anal fin rays	194	63-78	68.54	0.16	[2]60-73
Pectoral fin rays	196	10-13	11.83	0.05	[1]11-13
Gill rakers:					
Lower arch	196	14-19	16.31	0.08	
Upper arch	196	4- 7	5.59	0.05	
Vertebrae	195	40-43	41.34	0.04	[3]40-42
Morphometric:					
Standard length/head length	235	3.64- 4.30	3.96	0.01	[2,4] 3- 4
Head length/upper jaw length	235	1.54- 2.26	2.05	0.005	[2]2- 2.26

[1]Ginsburg (1952)
[2]Hildebrand and Schroeder (1928).
[3]Deubler (1958).
[4]Jordan and Evermann (1898)

TABLE 6.—A comparison of some summer flounder meristic characters between Delaware Bay (present study), Chesapeake Bay (Ginsburg 1952), and North Carolina [1 (Deubler 1958), 2 (Ginsburg 1952), and 3 (Woolcott et al. 1968)].

	Dorsal fin rays		Anal fin rays		Vertebrae		Gill rakers			
							Upper arch		Lower arch	
Location	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Delaware Bay	88.9	2.8	68.5	2.3	41.3	0.6	5.6	0.7	16.3	1.1
Chesapeake Bay	88.6	2.6	68.6	2.3			5.6	0.6	16.5	0.9
N.C. (1)	89.0	2.7	68.4	2.6	41.3	0.5				
N.C. (2)	88.1	2.7	67.7	2.2			5.0	0.7	15.6	1.3
N.C. (3)	88.4	1.4	68.3	1.2	41.2	0.6	5.2	1.0	14.6	1.5

	Gill rakers											
	Anal fin rays					Upper arch				Lower arch			
Location	Del. Bay	Ches. Bay	N.C. (1)	N.C. (2)	N.C. (3)	Del. Bay	Ches Bay	N.C. (2)	N.C. (3)	Del. Bay	Ches. Bay	N.C. (2)	N.C. (3)
Delaware Bay				·				··				··	··
Chesapeake Bay				·				··	·			··	··
N.C. (1)													
N.C. (2)	·	·				··	··			··	··		·
N.C. (3)										··	··	·	

· = significant difference at 0.05 level.
·· = significant difference at 0.01 level.

the definitive number of gill rakers is not usually present until summer flounder are 18 mm standard length. Woolcott et al. used fish below this length, and this could account for the significant difference between their counts of lower arch gill rakers and the counts by Ginsburg (1952), also for fish from North Carolina.

Anal fin and gill raker data (Table 6) do suggest, however, that summer flounder from North Carolina belong to a population that is racially different from the population containing Chesapeake Bay and Delaware Bay flounder. This supports Smith's (1973) observation that there is mounting evidence for the existence of separate populations of summer flounder based on: 1) distribution of eggs and larvae, 2) meristic differences, 3) tag returns, and 4) commercial flounder landings. It is possible that separate populations or stocks exist because summer flounder undergo fairly rapid development, 74 to 94 h hatching time (Smith 1973), and conditions affecting egg and larval transport may minimize mixing between geographic areas. This possibility is suggested by Chang and Pacheco (1976) even though they assumed a unit stock for their population evaluation. There should be more research into the possibility of multiple populations before final management recommendations are made.

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LARVAL DEVELOPMENT OF THE SPIDER CRAB, *LIBINIA EMARGINATA* (MAJIDAE)[1]

D. MICHAEL JOHNS[2] AND WILLIAM H. LANG[3]

ABSTRACT

Larval development of the spider crab, *Libinia emarginata*, consists of two zoeal stages and megalopa. Laboratory-reared larvae (South Carolina and Rhode Island) are described and compared with planktonic larvae from Narragansett Bay, R.I. No significant variations in morphology were found between laboratory-cultured larvae and "wild" larvae from plankton catches; first stage zoea from South Carolina were smaller than Rhode Island specimens. Using *Artemia* diets, the best percentage survival in culture was found to be 20°C for Rhode Island larvae and 25°C for South Carolina larvae. Zoeal stages show little difference from larvae of *L. dubia*; however, the megalopae of the two species can be differentiated by the number of protuberances on the cardiac region of the carapace.

Larval stages have previously been described for a number of species from the family Majidae (Sandifer and Van Engel 1971, 1972). For the genus *Libinia* only two complete descriptions have been published. Boschi and Scelzo (1968) described larval stages of *L. spinosa* from Mar del Plata Harbor, Argentina; and Sandifer and Van Engel (1971) described the larval stages of *L. dubia* from Chesapeake Bay. Larvae of *L. erinacea* have been described by Yang (1967), but the results remain unpublished. In all cases, the larval development consists of two zoeal stages and a megalopa.

Adult *Libinia emarginata* Leach range from Windsor, Nova Scotia, to the western Gulf of Mexico and are found in nearshore waters down to a depth of 29 m (Williams 1965). Although the larvae of *L. emarginata* have not been formally described, they have been successfully reared (J. D. Costlow, pers. commun.). Grassle (1968) studied heterogeneity of hemocyanins during ontogeny, but no attempt was made to describe development. In support of ongoing studies using *Libinia* larvae at this laboratory, the present study was undertaken to: 1) describe the larval stages, 2) compare morphology of laboratory cultured and field collected larvae, and 3) determine successful temperature-salinity rearing parameters and development times. Characteristics which distinguish *L. emarginata* larvae from the larvae of *L. dubia* and *L. erinacea* were also noted.

METHODS AND MATERIALS

Ovigerous females of *L. emarginata* were collected off Charleston, S.C., during fall 1975 and spring 1976, and in Narragansett Bay, R.I., during summer 1976. Females were isolated in chambers at 25°C (in South Carolina) or 20°-22°C (in Rhode Island) and 30‰. After hatching, zoeae were isolated into compartmentalized plastic boxes. Larvae were fed day old *Artemia* every other day following a change of water. Larvae reared at salinities other than 30‰ were brought to the appropriate levels (15, 20, 40, or 45‰) using increment changes of 2.5‰ every 30 min. Larvae reared at temperatures other than hatching temperature were brought to the test temperature (15°, 20°, or 30°C) by placing larvae in environmental chambers and allowing them to equilibrate to these temperatures.

Field samples were obtained from surface plankton tows collected in Narragansett Bay during July and August 1976.

Drawings were made with the aid of camera lucida using exuviae and larvae fixed in 10% Formalin.[4] Carapace and total lengths were made with an ocular micrometer. Dry weights were determined with a Cahn Electrobalance on larvae

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[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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that were dried in an 80°C oven for 24 h. The weights for each stage were calculated from three samples of five zoeae each.

One-way analysis of variance was computed on carapace length measurements taken on larval stages from South Carolina reared, Rhode Island reared, and field samples. If significant differences (at $P = 0.05$) were found within stages, a Scheffe Posterior comparison was used to determine where the differences lay (Nie et al. 1975).

The following abbreviations were used in all descriptions: AN1 = antennule, AN2 = antenna, MN = mandible, MAX1 = maxillule, MAX2 = maxilla, MXP1 = first maxilliped, MXP2 = second maxilliped, MXP3 = third maxilliped, P1 to P5 = pereopods 1 to 5, PL2 to PL6 = pleopods on abdominal somites 2 to 6. Types of setae specified are as described by Bookhout and Costlow (1974).

RESULTS

Development

Development times in both the South Carolina and Rhode Island reared larvae vary with temperature and salinity. In the South Carolina larvae, optimal and most advanced development occurred at 25°C and 30‰. At these conditions, the second stage appeared at day 3, megalopa at day 6 and first crab at day 14. In other conditions tested, development did not continue past the megalopa (Table 1).

In the Rhode Island reared larvae, complete development occurred only at 20°C and 30‰ with the second zoeal stage appearing at day 5, megalopa at day 8, and first crab at day 14. With other conditions tested, development was varied (Table 1).

South Carolina reared larvae tended to be smaller than both Rhode Island reared and field samples (Table 2). With statistical analysis, this difference is significant in stage I ($P<0.05$) but only between South Carolina reared and Rhode Island reared. At no other stage were the size variations found to be significant.

TABLE 1.—Time to various developmental stages (in days) for the spider crab, *Libinia emarginata*, reared at various temperature-salinity combinations in both South Carolina and Rhode Island.

Rearing site	Temperature-salinity combination	No. of larvae	Stage		
			II	Megalopa	1st crab
South Carolina	15°C-30‰	36	12	27	(1)
	20°C-30‰	36	7	12	(1)
	25°C-15‰	54	(1)		
	25°C-20‰	54	3	8	(1)
	25°C-30‰	54	3	6	14
	25°C-40‰	54	3	7	(1)
	25°C-45‰	54	4	8	(1)
	30°C-30‰	36	(1)		
Rhode Island	15°C-30‰	60	(2)		
	20°C-30‰	60	5	8	14
	25°C-30‰	60	4	(1)	

[1]All larvae had died prior to this stage.
[2]Second stage was not reached by day 15.

TABLE 2.—Comparison of carapace lengths for South Carolina reared, Rhode Island reared, and field sample larvae of *Libinia emarginata*.

Stage	Item	South Carolina reared	Rhode Island reared	Field samples
Zoea I*	$\bar{x}$ (mm)	[1]0.75	[1]0.78	0.775
	SD (mm)	0.019	0.020	0.028
	N	10	10	13
Zoea II	$\bar{x}$ (mm)	0.94	0.94	0.96
	SD (mm)	0.02	0.038	0.035
	N	7	14	11
Megalopa	$\bar{x}$ (mm)	1.16	1.21	1.20
	SD (mm)	0.049	0.064	0.001
	N	4	3	4

*Indicates significant differences within a stage by one-way analysis of variance ($P = 0.05$).
[1]Significant differences exist between the two means, according to Scheffe's Posterior comparison.

Larval Description

Two zoeal stages and one megalopa were obtained during the rearing period. Mandibles of the zoea are without palps and have a complex triangular biting surface. Since, in these stages, mandibles appear to have little diagnostic value and are difficult to accurately portray, they have been omitted from the following description.

Zoea I

Size and weight—Average carapace length, 0.78 mm (range 0.76-0.80 mm), average total length 2.19 mm (range 2.00-2.30 mm). Average dry weight 0.0214 mg (range 0.0200-0.0224 mg).

Carapace (Figure 1A, B) with dorsal and rostral spines; lateral spines absent. Dorsal spine long and slightly curved posteriorly; rostral spine nearly as long as antennule and slightly curved inward. Carapace large and somewhat rounded; 7 small plumose setae along the ventrolateral margin of carapace. Eyes sessile.

Abdomen (Figure 1C) with 5 somites; 6th somite fused to telson. Somite 2 with small anteriorly curved knobs on each side of lateral surface; somites 3-5 with pair of small posterolateral spines. Bifurcate telson; each furca bearing 1 spine. Inner

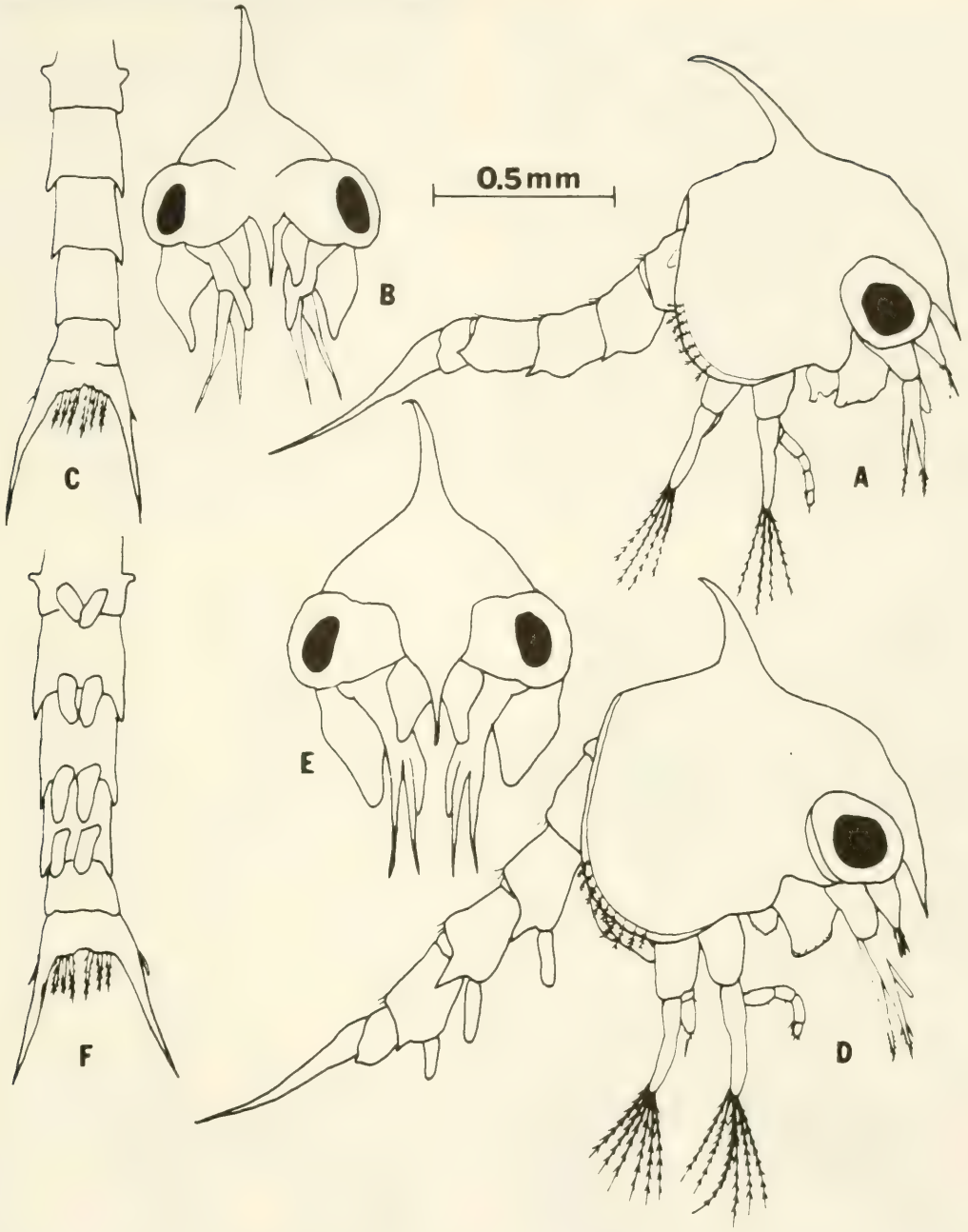

FIGURE 1.—*Libinia emarginata* zoea I and II. (A) lateral view of stage I, (B) front view of stage I, (C) dorsal view of abdomen at stage I, (D) lateral view of stage II, (E) front view of stage II, (F) dorsal view of abdomen at stage II. All unmarked scales = 0.1 mm.

margin of telson fork bearing 6 spines of approximately the same length.

AN1 (Figure 2C)—Uniramous, unsegmented, and conical with 2 long aesthetascs, 2 smaller aesthetascs, and one simple setae on the terminal end.

AN2 (Figure 2D)—Protopodite long, ending in a point with 2 rows of spinules distally, small endopodite bud near base. Exopodite long, spinulose distally; 2 small spines just subterminal, innermost spinulose.

MAX1 (Figure 2F)—Endopodite 2-segmented; proximal segment with 1 long simple or sparsely plumose seta, distal segment with 4 terminal setae (2 plumose, 2 plumodenticulate) and 1 subterminal plumose seta. Basal endite with 4 plumodenticulate cuspidate and 2 plumodenticulate terminal setae and 1 subterminal plumose seta; smaller coxal endite with 5 plumose setae and 2 simple setae.

MAX2 (Figure 2E)—Scaphognathite with 9 plumose marginal setae and a plumose apical tip. Endopodite simple with 4 (rarely 5) terminal plumodenticulate setae and 1 simple seta. Basal endite slightly bilobed; 4-5 plumodenticulate setae on distal lobe and 5 (rarely 4) plumodenticulate setae on proximal lobe. Coxal endite bilobed; 3-4 plumose setae on distal lobe and 4 plumose setae on proximal lobe.

MXP1 (Figure 2A)—Exopodite with 4 long, plumose natatory setae. Endopodite 5-segmented; setation formulae (proximal to distal): 3, 2, 1, 2, 5. Terminal segment with 5 setae (4 multidenticulate and 1 short, simple). Basiopodite with up to 9 setae.

MXP2 (Figure 2B)—Exopodite with 4 plumose

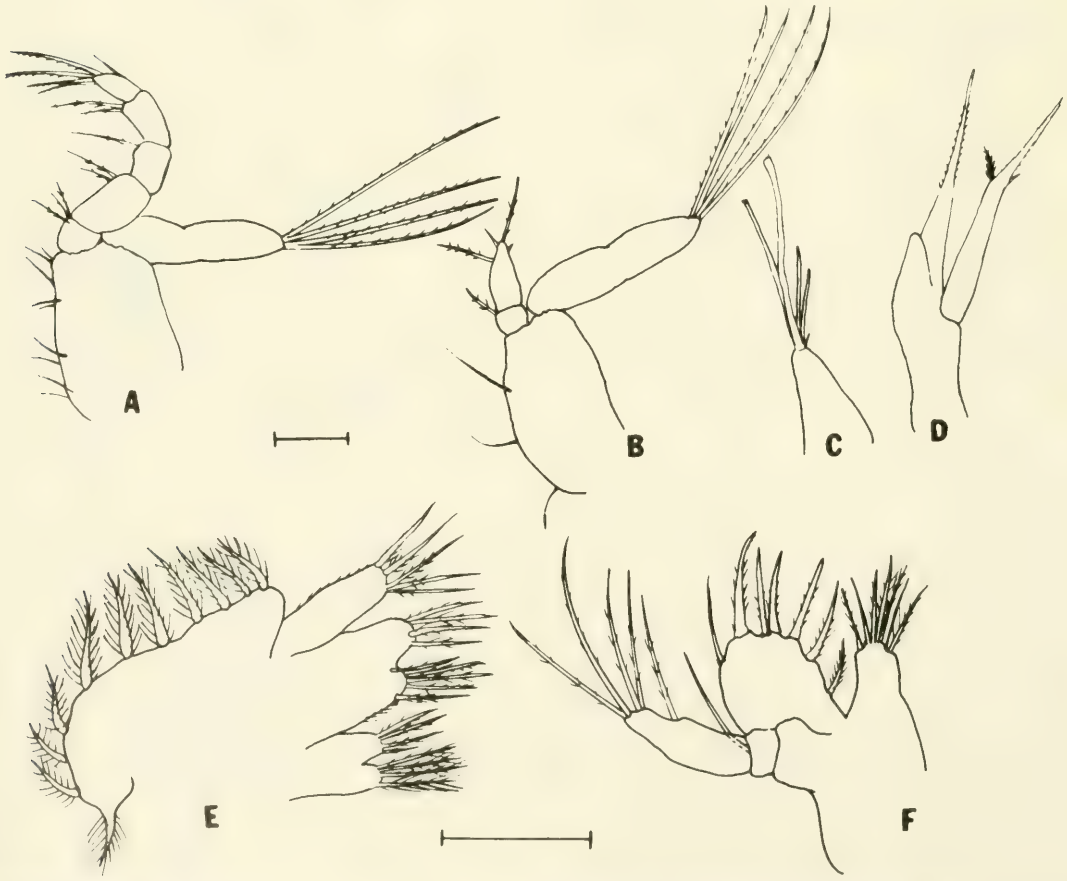

FIGURE 2.—*Libinia emarginata*. Appendages of stage I zoea. (A) first maxilliped, (B) second maxilliped, (C) antennule, (D) antenna, (E) maxilla, (F) maxillule. All unmarked scales = 0.1 mm.

natatory setae. Endopodite 2-segmented; terminal segment with 4 setae (2 plumodenticulate and 2 simple). Basiopodite with 3 setae.

Zoea II

Size and weight—Average carapace length, 0.94 mm (range 0.89-0.98 mm), average total length 2.69 mm (range 2.56-2.82 mm). Average dry weight, 0.0654 mg (range 0.0613-0.0712 mg).

Carapace (Figure 1D) same as for stage I. Dorsal spine proportionately shorter and stouter than before. Ventrolateral margin now with 8-10 small plumose setae. Eyes stalked.

Abdomen (Figure 1F) with 6 somites. Somite 2 with small anteriorly curved knobs as before. Somites 2-5 with 2 pleopod buds ventrally. Telson as in stage I.

AN1 (Figure 3C)—With 2 long, thick aesthetascs, 4 smaller aesthetascs, and 1-2 simple setae or thin aesthetascs on terminal end.

AN2 (Figure 3D)—Protopodite same as before, endopodite bud at least half length of protopodite. Exopodite same as before.

MAX1 (Figure 3F)—Endopodite same as before. Basal endite with 8 terminal setae (5 denticulate cuspidate and 3 plumodenticulate), and 2 subterminal plumose setae; coxal endite with 8 setae (5 plumose and 3 simple).

MAX2 (Figure 3E)—Scaphognathite with 16 (in South Carolina reared) or 20 (in Rhode Island reared and field samples) plumose marginal setae. Endopodite with basal endite and coxal endite same as in stage I.

MXP1 (Figure 3A)—Exopodite with 6 large plumose natatory setae. Endopodite same as before. Basiopodite with up to 10 setae.

MXP2 (Figure 3B)—Exopodite with 6 large,

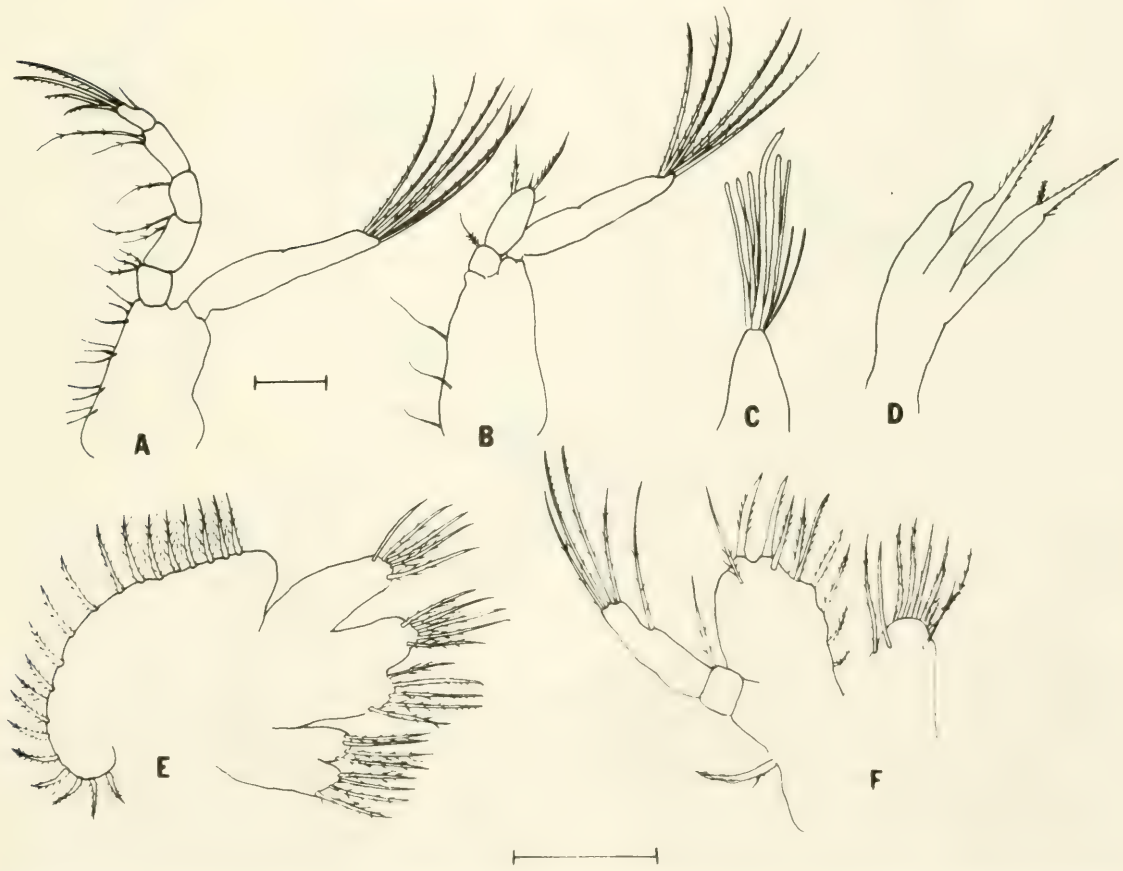

FIGURE 3.—*Libinia emarginata*. Appendages of stage II zoea. (A) first maxilliped, (B) second maxilliped, (C) antennule, (D) antenna, (E) maxilla, (F) maxillule. All unmarked scales = 0.1 mm.

plumose natatory setae. Endopodite and basiopodite same as before.

Megalopa

Size and weight—Average carapace length, 1.21 mm (range 1.16-1.28 mm), average total length 2.14 mm (range 2.07-2.17 mm). Average dry weight 0.205 mg (range 0.145-0.259 mg).

Carapace (Figure 4A, B) without spines; short rostrum tapers to blunt tip. Median line of carapace depressed between eyes with 2 partially connected protuberances along gastric region, paired protuberances at cardiac region and slight protuberance at posterior border. Lateral carapace region with 3 paired protuberances, surface somewhat expanded over posterolateral area.

Abdomen (Figure 4B) with 6 somites plus telson.

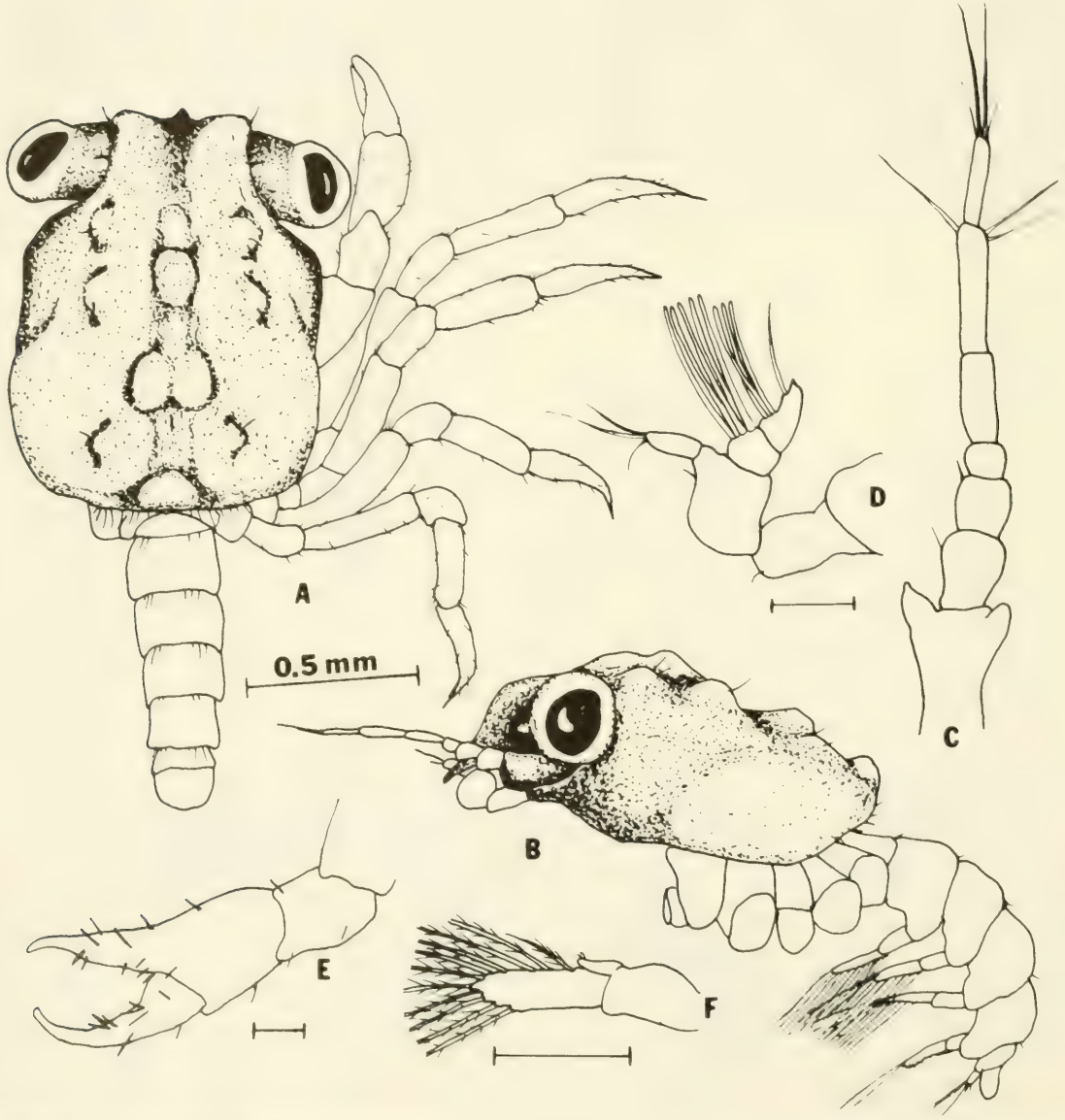

FIGURE 4.—*Libinia emarginata* megalopa. (A) dorsal view, (B) lateral view, (C) antenna, (D) antennule, (E) cheliped, (F) pleopod. All unmarked scales = 0.1 mm.

AN1 (Figure 4D)—Peduncles 3-segmented; basal segment bare, second and third segment with 1 short seta each. Inner flagellum unsegmented with 3 terminal simple setae; dorsal flagellum 2-segmented proximal segment with 5 aesthetascs; distal with 3 aesthetascs and 1 subterminal simple seta.

AN2 (Figure 4C)—Peduncle 3-segmented. Flagellum 4-segmented, with 2 distal segments having 3 subterminal and 4 terminal simple setae, respectively.

MN (Figure 5A)—Palp 3-segmented with 5 terminal setose setae.

MAX1 (Figure 5B)—Endopodite unsegmented with 2-3 terminal simple setae. Basal endite with 14 processes (6 plumodenticulate cuspidate, 6 plumodenticulate, 2 short multidenticulate) and 2-3 marginal plumose setae; coxal endite with 3 plumodenticulate and 3 simple terminal setae and 4 subterminal plumose setae.

MAX2 (Figure 5C)—Scaphognathite with 31-33 (in South Carolina reared) or 33-35 (in Rhode Island reared and field samples) plumose marginal setae. Endopodite with 0-1 seta. Basal endite bilobed; distal portion and proximal portion with 6-7 plumodenticulate or plumose setae each. Coxal endite bilobed; distal portion with 3 plumose setae and proximal portion with 4 plumose and 1 simple setae.

MXP1 (Figure 5D)—Exopodite 2-segmented, proximal segment with 1 plumose seta; distal segment with 5 plumose and 1 simple setae. Endopodite unsegmented with 1-3 terminal setae. Basal endite with 8-10 plumodenticulate setae; coxal endite with 6 plumodenticulate and 1 plumose setae. Epipodite with 4 long simple setae.

MXP2 (Figure 5E)—Exopodite 2-segmented; distal segment with 5-6 long plumose setae. Endopodite 4-segmented; setation formulae (proximal to distal) 0, 1, 3, 6. Distal setae, 5 plumodenticulate cuspidate, 1 simple.

MXP3 (Figure 5F)—Exopodite 2-segmented; terminal segment with 3-4 long plumose and 2 small simple terminal setae. Endopodite 5-segmented; setation formulae (proximal to distal) 9-10, 7-8, 4, 6, 4, mostly plumodenticulate or serrate plumose setae. Epipodite with 3 terminal and 3 subterminal multidenticulate setae.

P1 to P5 (Figure 4A, E)—Moderately setose, cheliped similar to adult form.

PL2 to PL6 (Figure 4F)—Exopodite 2-segmented; plumose natatory setae on distal segment varies from 11 (PL2) to 8 (PL5). Endopodite small with 2 small hooks.

Zoeal Chromatophores

Libinia emarginata larvae are sparsely pigmented in freshly sacrificed specimens. Chromatophore color ranges from orange to a dark brown-red. Distinctive pigment areas with little individual variation include an orange spot at the posterior dorsal spine base, a deep red area posterior to the eye base, a large distinctive red spot on the posterolateral carapace region near the carapace setae and red pigmentation of the mandibles. The abdomen is pigmented in the central ventral area of each segment juncture. Additional pigment spots occur on the carapace and appendages but do not appear consistent in location or occurrence.

DISCUSSION

There is only a narrow range of temperature-salinity conditions at which the larvae successfully develop in the laboratory. With South Carolina larvae, these conditions are 25°C and 30‰, while with Rhode Island larvae, maximum development occurs at 20°C and 30‰. The difference in these temperatures possibly reflects the influence of latitudinal separation on larval development, however, until critical experiments are undertaken, this cannot be confirmed (Vernberg 1962; Vernberg and Costlow 1966; Sastry 1970; Sastry and Vargo 1977). The larvae develop best in temperatures that represent the mean temperature during the larval season. Gravid *L. emarginata* were collected from May to September in South Carolina in coastal waters that had a mean water temperature near 25°C. In Rhode Island, gravid crabs were collected from July to August in bay and coastal waters that had a mean water temperature near 20°C.

The narrowness of successful rearing conditions may reflect inadequate rearing variables such as diet, substrate, water circulation, etc. (Roberts 1972; Sulkin 1975; Sulkin and Norman 1976), or reflect the habitat of *L. emarginata*. With larvae that develop entirely in bay or coastal waters, there follows a characteristic inability of larvae to develop successfully over wide ranges of temperature and salinity, while larvae from estuarine waters usually develop in a much wider range of temperatures and salinity. In the offshore

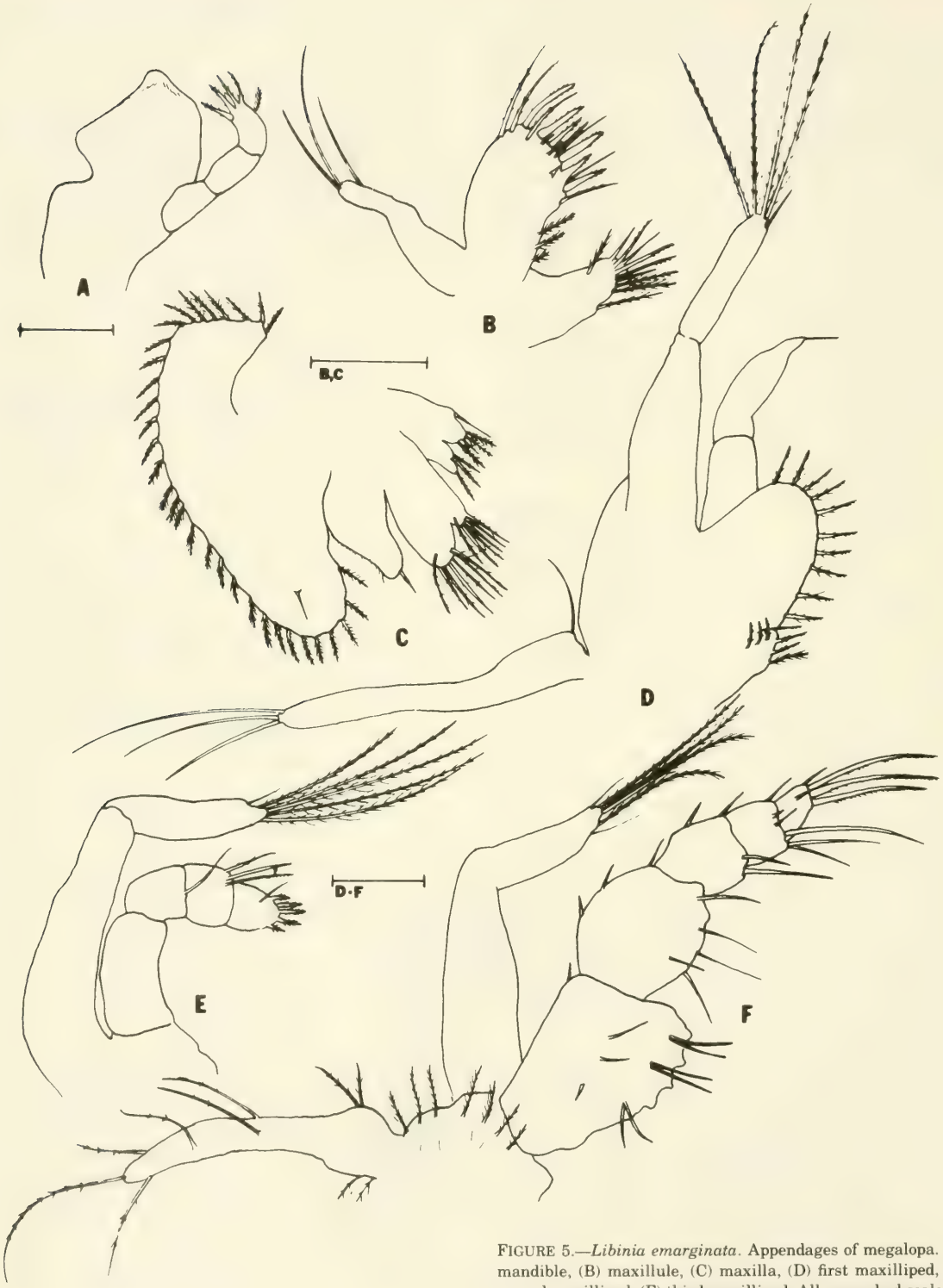

FIGURE 5.—*Libinia emarginata*. Appendages of megalopa. (A) mandible, (B) maxillule, (C) maxilla, (D) first maxilliped, (E) second maxilliped, (F) third maxilliped. All unmarked scales = 0.1 mm.

spawner, *Callinectes sapidus*, for example, larvae will complete early development only at 25°C and 31.1‰ (Costlow and Bookhout 1959) while an estuarine xanthid, *Rhithropanopeus harrisii*, completes development at temperatures of 20°, 25°, and 30°C and salinities between 2.5 and 40‰ (Costlow et al. 1966). Throughout this study, all gravid females were collected in near coast bay or open coastal waters (>30‰ salinity).

The duration of development within the genus *Libinia* also varies. Boschi and Scelzo (1968) reported that development for *L. spinosa* required 20-30 days (at 20°C) or an average of 8-10 days per stage. *Libinia erinacea* required 14 days (at 20°C) or 9 days (at 25°C) to reach first crab stage (Yang 1967). Sandifer and Van Engel (1971) reported that *L. dubia* needed only 9 days (at 25.5°-28.5°C) for larval development. *Libinia emarginata* is intermediate with at least 14 days needed to reach first crab stage. As pointed out by Sandifer and Van Engel (1971), these differences in development times may be explained, in part, by rearing temperatures. For *L. erinacea*, total development time is reduced by 5 days with a 5°C increase in temperature. However, other factors must also play a role in development for *L. spinosa* and *L. erinacea* reared at the same temperature (20°C) and given the same food source (*Artemia*) still showed a 6- to 16-day difference in development times.

The number of larval stages for *L. emarginata* is typical for the family Majidae (Gurney 1942; Hart 1960). Larvae from the three sources examined showed few differences. South Carolina larvae tended to be slightly smaller than Rhode Island and field samples (Table 2). Morphology of larvae was virtually identical in all cases, except for the scaphognathite setal number being consistently lower in South Carolina larvae. In this case, reared larvae appear to represent accurate "mimics" of wild larvae, even to specific setal types. However, it is unknown if this similarity also pertains to physiological or behavioral parameters.

In comparing larval descriptions of *L. erinacea*, *L. dubia*, *L. spinosa*, and *L. emarginata*, we have found that carapace setation and armature of the abdominal somites are the most useful zoeal characters (Table 3). *Libinia erinacea* and *L. spinosa* may be distinguished by the presence of lateral spines on abdominal somite 2, as opposed to small knobs for *L. dubia* and *L. emarginata*. *Libinia spinosa* may be differentiated from *L. erinacea* by the lack of setation on the ventrolateral margin of the carapace. The first zoea of *L. dubia* and *L. emarginata* show no differences in general morphology and setal numbers. The second zoea of *L. emarginata* usually has 10 setae on the ventrolateral margin while *L. dubia* has 8 setae but as in stage I there appears to be no ready

TABLE 3.—Comparison of diagnostic characteristics for zoeal stages of *Libinia erinacea*, *L. spinosa*, *L. dubia*, and *L. emarginata*.

Species and stage	Dorsal spine	Abdominal somites		Carapace setation
		Somite 2	Somites 3-5	
L. erinacea:[1]				
Zoea I	Single, long, curved posteriorly, sometimes ending in short hook	Two lateral spines, one on each side, pointing posteriorly	Two medium spines, one on each side, pointing posteriorly	6 setae on ventrolateral margin
Zoea II	Same as zoea I	Same as in zoea I, but with pair of pleopod buds per somite	Same as in zoea I, but with pair of pleopod buds per somite	8 setae on ventrolateral margin
L. spinosa:[2]				
Zoea I	Same as in *L. erinacea*	Same as in *L. erinacea*	Two long spines, one on each side, pointing posteriorly	No setation on ventrolateral margin
Zoea II	Same as in *L. erinacea*	Same as in *L. erinacea*	Same as in zoea I, but with pair of pleopod buds per somite	No setation on ventrolateral margin
L. dubia:[3]				
Zoea I	Single, fairly long, curved posteriorly	Two small curved knobs, one on each side	Two small spines, one on each side, pointing posteriorly	6-7 setae on ventrolateral margin
Zoea II	Same as zoea I	Same as in zoea I, but with pair of pleopod buds per somite	Same as in zoea I, but with pair of pleopod buds per somite	7-8 setae on ventrolateral margin
L. emarginata				
Zoea I	Single, long, slightly curved posteriorly	Same as in *L. dubia*	Same as in *L. dubia*	7 setae on ventrolateral margin
Zoea II	Short and stout	Same as in *L. dubia*	Same as in *L. dubia*	8-10 setae on ventrolateral margin

[1]From Yang (1967).
[2]From Boschi and Scelzo (1968).
[3]From Sandifer and Van Engel (1971).

TABLE 4.—Average carapace lengths, total lengths and dry weights for the larval stages of *Libinia emarginata, L. dubia, L. erinacea,* and *L. spinosa.*

Species	Carapace length (mm)			Total length (mm)			Dry weight (mg)		
	Zoea I	Zoea II	Megalopa	Zoea I	Zoea II	Megalopa	Zoea I	Zoea II	Megalopa
L. emarginata	0.78	0.94	1.21	2.19	2.69	2.14	0.0214	0.0654	0.205
L. dubia[1]	0.81	0.97	1.16	2.35	2.78	2.11	—	—	—
L. erinacea[2]	0.88	1.03	1.24	—	—	—	—	—	—
L. spinosa[3]	0.80	0.96	1.30	2.30	2.80	3.10	—	—	—

[1]From Sandifer and Van Engel (1971).
[2]From Yang (1967).
[3]From Boschi and Scelzo (1968).

means to distinguish the species. *Libinia dubia* zoea, as described by Sandifer and Van Engel (1971), are larger than *L. emarginata* zoea (Table 4), but statistical analysis of various samples would be needed to determine if a consistent size difference exists. Differences in setal types may also occur, but these have not been described for *L. dubia*. As with larvae of various species of *Uca* (Hyman 1920), a rapid, reliable means to distinguish *L. emarginata* and *L. dubia* larvae to species does not exist.

Megalopae of all four species, however, are distinguishable. *Libinia spinosa* has a distinct dorsal spine which curves posteriorly (Boschi and Scelzo 1968) while the dorsal spine of *L. erinacea* is long and upright (Yang 1967). *Libinia dubia* and *L. emarginata* megalopae both lack a dorsal spine. The median cardiac protuberance of the *L. dubia* megalopa is single but is paired in *L. emarginata*. This difference is relatively easy to observe, thus unlike zoeal stages, *L. dubia* and *L. emarginata* megalopae may be identified to species.

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THE RIBBONFISH GENUS *DESMODEMA*, WITH THE DESCRIPTION OF A NEW SPECIES (PISCES, TRACHIPTERIDAE)

RICHARD H. ROSENBLATT[1] AND JOHN L. BUTLER[2]

ABSTRACT

The genus *Desmodema* is unique within the Trachipteridae in that the upper caudal lobe, borne on the second ural centrum, is not upturned, and the lower caudal lobe, borne on the first ural centrum in other trachipterids, is absent, and in that there are seven dorsal pterygiophores before the first neural spine. *Desmodema lorum* n.sp. can be distinguished from *D. polystictum* (Ogilby) on the basis of having more vertebrae, fewer caudal rays, a longer tail, and the snout longer than the eye diameter. *Desmodema polystictum* is probably circumtropical; *D. lorum* is restricted to the North Pacific Ocean. The species of *Desmodema* have a distinctive prejuvenile phase characterized by polka dots on the sides, long pelvic fins, a relatively short tail, and elongation of the first six dorsal rays. Metamorphosis is abrupt and involves loss of the pelvic fins, elongated dorsal rays and polka dots, and a great lengthening of the tail. It is suggested that metamorphosis accompanies movement to a deeper habitat. The elongated tail is related to extension of the lateral-line sensory system. On the basis of joint possession of a dermal tubercle and pore system and an abruptly constricted body, *Desmodema* and *Zu* are regarded as related. *Desmodema*, but not *Zu*, agrees with *Regalecus* in the arrangement of the dorsal pterygiophores.

The genus *Desmodema* was erected for the reception of *Trachypterus jacksoniensis polystictus* Ogilby (Walters and Fitch 1960). Fitch (1964) subsequently redescribed *Desmodema polystictum*, mainly utilizing material from the northeast Pacific, and placed *Trachypterus misakiensis* Tanaka, 1908 and *T. deltoideus* Clark, 1938 in its synonymy. Our interest arose from the observation that two recently collected specimens had what appeared to be anomalously low vertebral counts. This initiated the present study, which has revealed the existence of two species, one of them undescribed. In addition to distinguishing and describing the species, our material has allowed us to amplify the generic description of *Desmodema* and to detail some of the remarkable ontogenetic changes undergone by its species.

MATERIALS AND METHODS

Specimens used in this study are housed in the following institutions: California Academy of Sciences (CAS), Department of Biology, University of California, Los Angeles (UCLA), Natural History Museum of Los Angeles County (LACM), and Scripps Institution of Oceanography (SIO). In the material list the first length measurement is the snout-vent length (SV), the second the standard length (SL). A single value indicates snout-vent length of a broken specimen.

Because of the delicacy of the species, most of the specimens were damaged in some way, and not all counts and measurements were made on all specimens. In particular, fin lengths represent minimum measurements, since all fins seem to have been broken to some degree. No specimen appeared to have unbroken pelvic fins. Measurements are self-explanatory and were taken with flat-point dividers or dial calipers. Vertebral counts were taken from radiographs or cleared and stained material. Dorsal rays could be enumerated on only a few specimens.

RESULTS

Desmodema Walters and Fitch

Desmodema Walters and Fitch 1960. Type-species *Trachypterus jacksoniensis polystictus* Ogilby 1897, by original designation.

Diagnosis.—A trachipterid with 4-10 caudal rays, the caudal on the same axis as the caudal peduncle, all caudal rays borne on terminal centrum, no lower caudal lobe. Seven dorsal pterygiophores before first neural spine. Body con-

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stricted behind anus, tail exceedingly elongated in juveniles and adults. Young with numerous dark round spots. Skin of adults pierced by numerous pores.

Description—Body strongly compressed laterally, postanal portion of body narrowing into a whiplike tail in juveniles and adults (posterior vertebrae about four times as long as 14th vertebra). Posterior region of body of larvae and prejuveniles narrow, but not exceedingly elongate (posterior vertebrae shorter than 14th vertebra). Seven pterygiophores before first neural spine, one or two pterygiophores between first and second neural spines. First pterygiophore closely applies to back of skull, no predorsal bones. Anterior five or six dorsal rays elongated in larvae and prejuveniles to form a dorsal pennant; these rays completely lost in adults. Pelvics long and fanlike in young, absent in adults. Caudal well developed, of 4-10 unbranched rays, parallel to axis of tail. Caudal rays all borne on last ural centrum, no ventral caudal lobe (Figure 1).

Fin rays with a lateral row of small spines, these weak or absent on posterior pelvic rays, middle caudal rays, and pectoral rays. Each dorsal ray anterior to elongated tail portion of body with a single laterally directed stout spine on either side of the base.

Lateral line ending at caudal base, lateral-line scales with a pair of spines. Body otherwise scaleless at all sizes (*D. polystictum*), or young covered with scales, each with a pair of longitudinal spinous ridges (*D. lorum*). Skin of adults with cartilaginous tubercles, and pierced by numerous pores (Walters 1963). No enlarged tubercles on ventral midline.

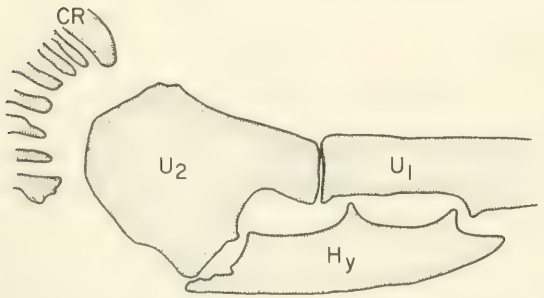

FIGURE 1.—Caudal skeleton of *Desmodema polystictum*, SIO 73-340. Camera lucida drawing at 25× magnification. Only bases of caudal rays shown. CR, caudal ray; Hy hypural; U_1, first ural centrum; U_2, second ural centrum and hypural.

Two nostrils in prejuveniles, the posterior just before anterior margin of eye; posterior opening obliterated in juveniles and adults. Nasal epithelium without ridges or folds at all sizes. Head bones cancellous and ridged. Mouth strongly oblique. Teeth restricted to one to four in each premaxilla and two enlarged, recurved fangs on mandible, one on either side of symphysis. Gill rakers (2-3) + (9-10) usually 3 + 9, fleshy, distally expanded and leaflike. Rakers of upper limb with a few teeth. Pseudobranch well developed. Gas bladder present in small juveniles (to about 30 mm SV), rudimentary or absent in large juveniles and adults.

Very young silvery, prejuveniles silvery with profuse dark spotting, adults without spots.

Growth changes.—Although we have no material smaller than 18.9 mm SV, it appears that development from a silvery or transparent form with a triangular outline with the head deepest, into the polka-dotted, deep bodied prejuvenile is gradual. The transition from prejuvenile to juvenile is probably rapid and can fairly be termed a metamorphosis. There is a large-size gap in our material of *D. polystictum* (91-260 mm SV), but our material of *D. lorum* includes the appropriate size classes. The difference between the prejuvenile and the final body form can be seen in Figure 5. The two specimens are almost identical in snout-vent length. However, the upper specimen is essentially a miniature adult. The major differences are in the change in the ventral profile, elongation of the tail, increase in eye size, eruption of lower jaw teeth, and loss of the spots, pelvic fins, and posterior nostril. Juveniles, including our largest (173 mm SV) have an elongate opening not yet covered over by the skin at the position of the pelvic fins, indicating that loss of the pelvics may be rapid, and from the base.

Walters (1963) indicated that juveniles of *D. polystictum* are scaled, but that adults are scaleless, and have cartilaginous tubercles and a subdermal canal system connected to the surface by numerous pores. In our material of *D. lorum* an 18.5-mm SV silvery individual lacks both scales and tubercles. An individual 36 mm SV is scaled, but lacks tubercles, and in another (36.5 mm SV), tubercles are present ventrally, and on the sides behind the head. Our largest polka-dotted prejuvenile is 95 mm SV. The upper sides are scaled; the remainder of the body is covered with tubercles and the subcutaneous canal system is well

developed, with surface pores present. A juvenile of 104 mm SV has scales along the dorsal base, and one of 131 mm SV lacks scales and has tubercles and pores over the entire body.

Desmodema polystictum does not agree with *D. lorum* in the course of development of the tubercles and pore system. None of our specimens has scales. Instead tubercles are developed in a specimen of 36 mm SV, and tubercles and pores are present in an individual of 42 mm SV. Walters (1963) was unaware of the existence of the two species of *Desmodema* and his figure 1 was undoubtedly based on a juvenile of *D. lorum*.

In juveniles the first six dorsal rays are elongated (broken in all our specimens). These rays, which are borne on the pterygiophores before the first neural spine, are lost, and in adults represented by a stiffening in the skin. The recurved, fanglike lower jaw teeth first appear at a snout-vent length of about 100 mm.

Life history and behavior.—We lack data from closing nets, and thus have no precise information on depth of capture of our material. Fitch and Lavenberg (1968) inferred that *Desmodema "polystictum"* lives "500 to 1,000 feet beneath the sea's surface" and Walters (1963) predicated his discussion of energetics on the assumption that *Desmodema* is mesopelagic. Harrison and Palmer (1968) speculated that *Desmodema*, which they described as "chocolate brown," might live deeper than its silvery relatives. Actually *Desmodema* is silvery and turns brown in preservative.

The number of polka-dotted juveniles of *D. polystictum* taken at or near the surface indicates that they probably mainly occupy the euphotic zone. The polka-dotted pattern would be maximally useful as protective coloration in the light-dappled environment near the surface. However, records (presumably juveniles) from stomachs of *Alepisaurus* (Fourmanoir 1969) suggest a considerable depth range. A number of juvenile *D. lorum* have been taken from albacore, *Thunnus alalunga*, stomachs, and others have been taken by gear fished near the surface. We see no reason to assume that the albacore had been feeding "far beneath the surface" (Fitch 1964); however, Fitch figured a metamorphosing juvenile of *D. lorum* from an *Alepisaurus* taken on a longline and listed four other such specimens, again indicating a wide depth range. Several of the metamorphosed specimens of *D. lorum* were taken by open nets fished to considerable depths. However, three of the largest specimens were taken in purse seines, indicating depths of capture of no more than 100 m. We have three adult *D. polystictum*: two were taken in nets towed in the upper 500 m, and one was taken in a purse seine.

Fitch's (1964) report on stomach contents provides equivocal evidence; *Idiacanthus* is a mesopelagic vertical migrator, but *Phronima sedentaria* occurs in the upper 300 m (Eric Shulenberger, Scripps Institution of Oceanography, pers. commun.). There is thus no objective evidence that either species of *Desmodema* lives below 500 m (although the possibility is not excluded). The species of *Desmodema* would seem to be members of the deep epipelagic group as defined by Parin (1968).

Keeping in mind the sketchy nature of the available data on depth distribution, the following hypothetical scheme is suggested for both species. The silvery young have a gas bladder. The large fins and the deep head and rapidly tapering body suggest that they are feeble swimmers. They are probably epipelagic. The polka-dotted prejuveniles probably occupy the euphotic zone. The tail is short and anguilliform propulsive waves could involve almost the entire body. The very elongate, fanlike pelvic fins and dorsal pennant indicate that swimming is normally slow and probably involves undulations of the dorsal fin, rather than the body.

With metamorphosis the dorsal pennant and the pelvic fins are lost, the latter dropping off entirely. The tail rapidly elongates at this time (see Figure 5). The polka-dotted pattern is also lost, but more gradually. The greatly elongated tail with its associated dorsal rays would produce drag during active swimming, but probably less so than in *Trachipterus*, in which the posterior part of the body is deeper. We propose that adult *Desmodema* normally occupy the twilight zone of a few hundred meters, where they hover, probably in a head-up posture, maintaining position by undulations of the dorsal fin. Rapid bursts of anguilliform swimming would accompany prey capture or predator avoidance. The tubercle and pore system might act to maintain laminar flow during burst swimming, as hypothesized by Bone (1972) for the oilfish, *Ruvettus*.

The elongate tail of *Desmodema* can be related to the hypothesized mode of life. The lateral line runs the length of the tail, ending at the caudal. The tail then serves the function of greatly extending the lateral line, and in effect provides an an-

tenna for the reception of water displacement and low frequency sound. In this connection it may be pointed out that in the related *Stylephorus chordatus* the lateral line is continued onto the exceedingly elongated caudal filament (R.H. Rosenblatt pers. obs.). *Stylephorus* has tubular eyes directed forward, and it is assumed that it maintains a vertical posture in the water (Marshall 1971:44). That elongate bodies in deep-sea and pelagic fishes are related to a sensory function has been suggested by Wynne-Edwards (1962:80).

Our presumption is that adult *Desmodema* hover vertically, visually seeking prey silhouetted against downwelling light. The lateral-line system of the tail would be used to sense predators approaching beneath the field of view of the eyes. Undulations of dorsal fin would be used for position-holding and the lateral body musculature used for burst swimming for prey capture and predator avoidance.

This mode of life may predominate in the elongate trachipteroids. Nishimura (1963) has inferred a similar life-style for *Trachipterus ishikawai*. Adults of *Zu cristatus* have a long, thin tail, reminiscent of that of the species of *Desmodema*, and Clarke and Haedrich (in Gaul and Clark 1968) recorded the following observation: "A large oarfish, *Regalecus glesne*, was sighted at about 210 meters. It was hanging vertically in the water, head up, and appeared to be almost two meters in length . . . . The dorsal fin was moving continuously with wave-like motions progressing from the head end to the tail end, very much like the fin motions seen in file fish."

Distribution.—Desmodema polystictum is probably circumtropical, and *D. lorum* appears to be restricted to the northern Pacific (Figure 2). The most obvious feature of the distributions is the lack of sympatry. *Desmodema polystictum* is broadly distributed in the tropical Pacific; the northern and southernmost records for the species are in areas influenced by warm currents. *Desmodema lorum* on the other hand is mostly restricted to the cooler waters of the North Pacific. Twenty of the 21 eastern Pacific specimens were taken north of lat. 28°N, that is in areas north of the 20°C August surface isotherm and the 9°C 200-m isotherm. The single western Pacific capture (a metamorphosed juvenile) was in the area where the temperature at 200 m is about 16°C.

The only area of possible sympatry indicated is near Cape San Lucas, lower California, where there are several records of *D. polystictum* and a single record of *D. lorum*. Occurrence of the latter that far south may be related to transport by the California Current.

From Figure 2 it appears that both species of *Desmodema* are especially common in the eastern Pacific. The pattern of captures more likely reflects effort. Many of the specimens of *D. polystictum* have been taken incidentally by the purse seine tuna fishery, which is concentrated in the eastern tropical Pacific. Similarly the predominantly eastern records for *D. lorum* probably reflect the intensive collection effort in the region of the California Current.

The presence of *D. polystictum* in the Atlantic rests on the records of Leapley (1953) and Walters (1963). G. Krefft, Instit für Seefischeri, Hamburg, has informed us that the RV *Walter Herwig* has taken several specimens of *Desmodema* in the central and southern Atlantic, but that the material is not available for study at the present time.

Comparison and relationships.—Walters and Fitch (1960) distinguished *Desmodema* from *Trachipterus* primarily on the basis of the nature of the caudal fin (parallel to the body axis), the length of the gastric caecum (long), the absence of sharp-tipped midventral tubercles, and the presence of scales in *Desmodema*. The last character is not diagnostic, since our study indicates that *D. polystictum* lacks scales at all sizes. The caudal structure of *Desmodema* is unique in the Trachipteridae in that all of the caudal rays are borne on the terminal centrum and the hypural of the first ural centrum is rayless (Figure 1). Additionally, in the species of *Desmodema* there are seven pterygiophores before the first neural spine and one or two between the first and second neural spines, and in *Zu* and *Trachipterus* there is a single pterygiophore before the first neural spine, and nine between the first and second neural spines.

Walters (1963) regarded *Zu* as the most generalized and *Desmodema* as the most specialized of the three trachipterid genera. Despite the specializations unique to *Desmodema* and *Zu* respectively, present evidence indicates that the two genera are more closely related to each other than either is to *Trachipterus*. The most important indicator of relationship if the presence in both of the dermal tubercles in large prejuveniles, and tubercles and a cutaneous pore system in juveniles and adults. Dermal tubercles,

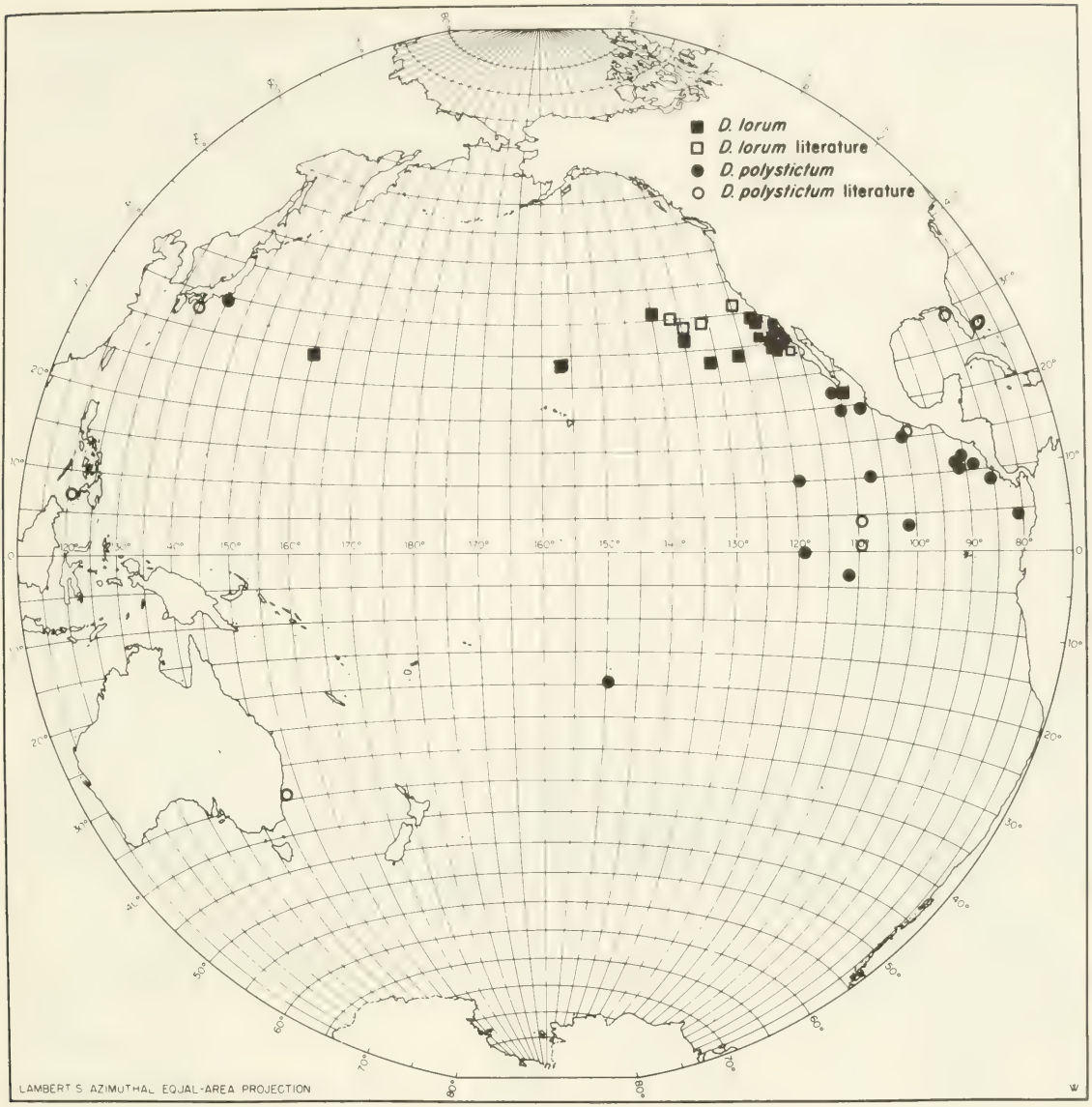

FIGURE 2.—Distribution of the species of *Desmodema*.

pores, and subdermal canals have not previously been reported for *Zu cristatus*. Instead the species has been described as having deciduous cycloid scales (Tortonese 1958; Walters and Fitch 1960; Palmer 1961; Fitch 1964). However, none of our specimens (8, 27.5-811 mm SL) has scales. Two specimens of about 40 mm SL have the skin intact and smooth, except for small tubercles on the lower sides anteriorly, with no trace of scales. Two specimens of 135 and 141 mm SL respectively have the body studded with soft tubercles, with a few interspersed pores; in a specimen of 210 mm SL both tubercles and pores are well developed. In the 811-mm SL adult the skin is superficially very similar to that of *Desmodema*. Our 135-mm SL specimen is from the Atlantic, so it does not appear that we are dealing with a difference between Atlantic and Pacific populations. We can only surmise that the tubercles and pores of *Zu* have been taken to represent scale pockets left behind by

deciduous scales. The "modified cycloid scales" mentioned by Harrisson and Palmer (1968) may have been the dermal tubercles.

In addition to the tubercle and pore system, *Zu* and *Desmodema* agree in two other specialized characters: the body is constricted behind the vent to form an elongated, slender tail, and there is a distinctive prejuvenile which metamorphoses into the juvenile phase.

In our interpretation, *Trachipterus* is the most generalized trachipterid genus, with *Desmodema* and *Zu* specialized in respect to the characters given above. *Desmodema* is advanced with respect to *Zu* in the loss of the lower caudal rays and great elongation of the tail, and probably in the crowding of the pterygiophores before the first neural spine. The significance of the difference in the relationship of the anterior dorsal fin pterygiophores between *Trachipterus* and *Zu* on the one hand and *Desmodema* on the other is difficult to interpret. In *Lophotus* there is a single rayless pterygiophore before the strongly forward-curved first neural spine, then about 15 uncrowded pterygiophores in the wide interspace between the first and second neural spines. The figure of *Regalecus* given by Parker (1886) clearly shows a condition much like that of *Desmodema*. Although the caudal of *Regalecus* has been described as lacking a ventral lobe, we find that two caudal rays are associated with the terminal centrum and four with the (ventral) hypural of the first ural centrum.

Desmodema polystictum (Ogilby)

Figures 3, 4

Trachypterus jacksoniensis polystictus Ogilby 1897:649; Newcastle, New South Wales, Australia; holotype, Australian Museum.

Trachypterus misakiensis Tanaka 1908:52, pl. IV, fig. 2, "shores of Misaki" Japan; holotype, Zool. Inst. University of Tokyo, No. 960. Herre and Herald 1951:318, fig. 3; 6°26′N, 121°35′E.

Trachypterus deltoideus Clark 1938:180; Rurutu Island, "Australs" (Tubuai Islands); holotype, CAS 5532.

Desmodema polysticta. Walters 1963:260; 28°58′N, 88°18′W; Integumentary system. Fitch 1964:230; in part, see synonymy of *D.*

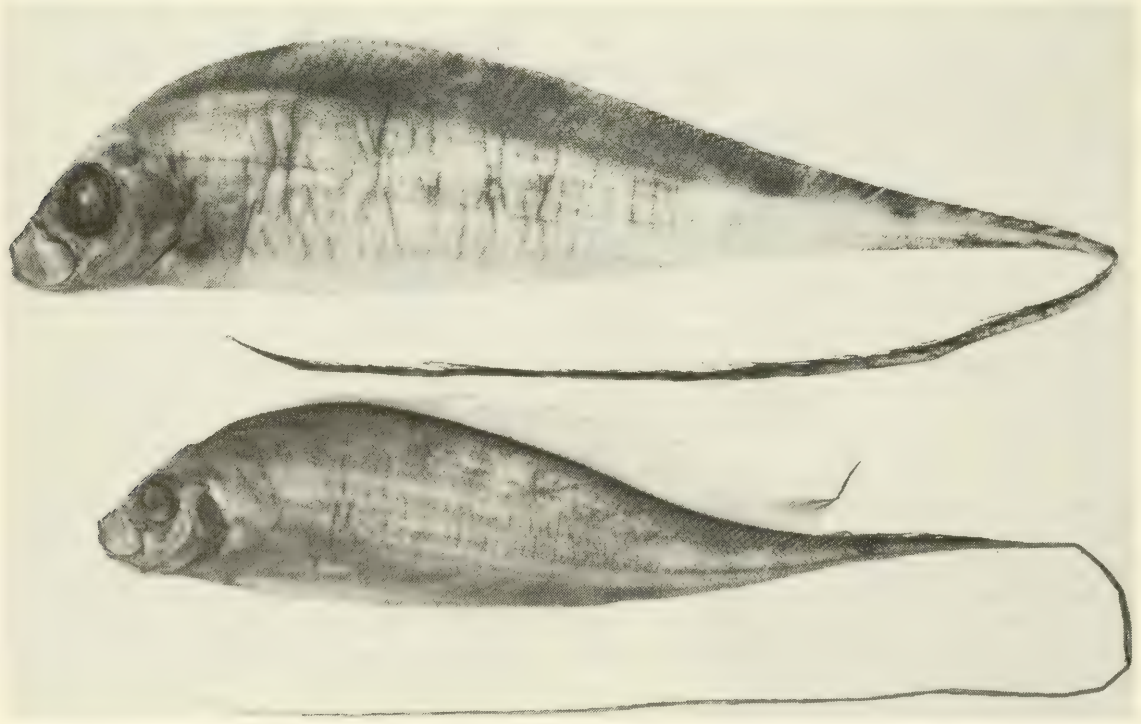

FIGURE 3.—Adults of the species of *Desmodema*. Upper figure *D. polystictum*, SIO 68-333, 1,040 mm SL. Lower figure holotype of *D. lorum*, USNM 216726, 1,098 mm SL.

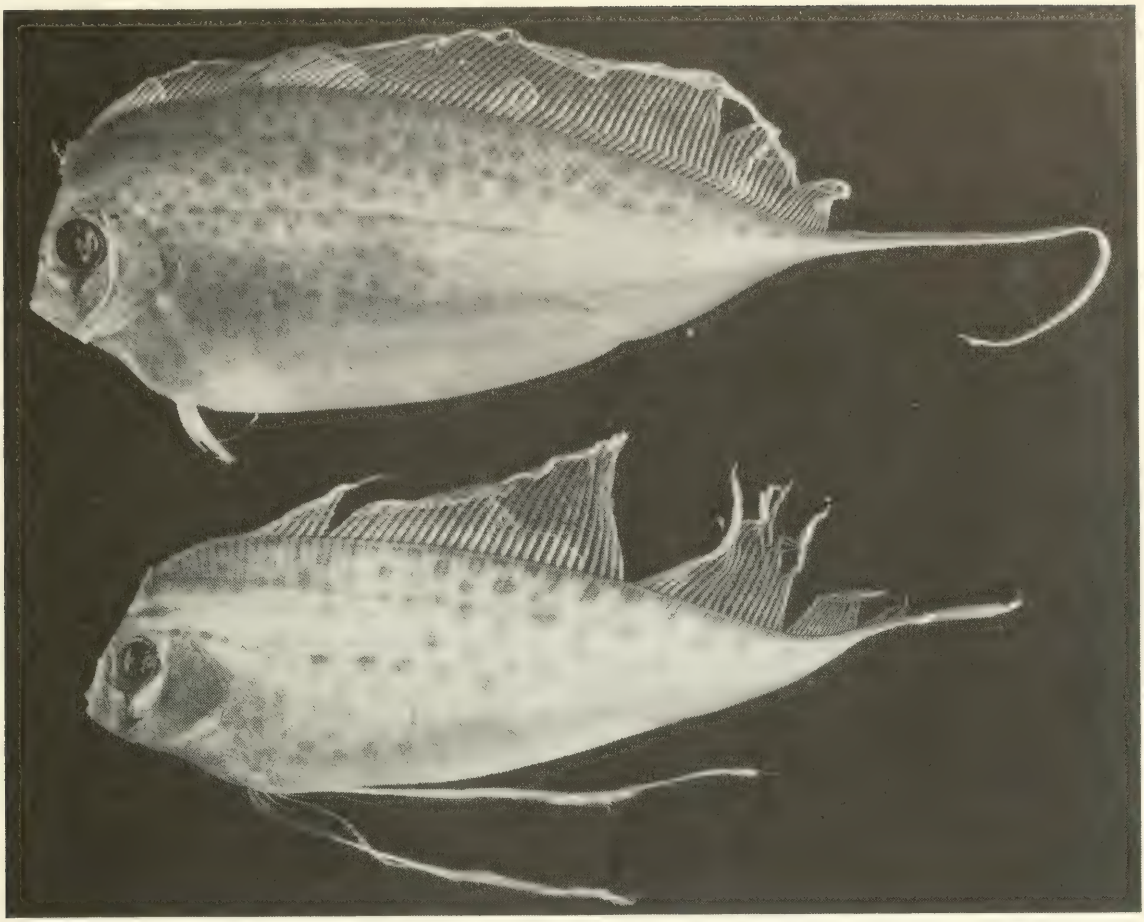

FIGURE 4.—Prejuveniles of *Desmodema*. Upper figure *D. lorum*, LACM 30597-1, 87 mm SV, 188 mm SL. Lower figure *D. polystictum*, SIO 75-55, 88 mm SV, 125 mm SL.

lorum. Fourmanoir 1969:36. Legand et al. 1972:383.

Trachipterus trachyurus, not of Poey. Leapley 1953:236; Fort Lauderdale, Fla.

Diagnosis.—A *Desmodema* with 71-74 total vertebrae (18-20 precaudal and 37-42 before the anus), 7-10 (usually 8) caudal rays, snout length less than eye diameter, attenuate tail in juveniles and adults (Figures 3, 7), and scales absent at all sizes.

Description of adult (see also Tables 1-3).—Ventral profile of body almost straight to anus, then tapering to elongate tail. Dorsal profile rising in a gentle curve to a point a little less than 1 head length behind head, then tapering rapidly to a point about 1½ head lengths behind anus, then tapering more gradually along elongate tail section. Tail long and straplike, postanal length almost two-thirds of standard length. Anus on ventral midline.

Head 2.2-2.5 in snout-vent length, and about 1.3 in greatest body depth. Eye large, diameter slightly greater than snout length. Ascending processes of premaxillae extending back to a point over posterior third of eye.

Dorsal origin over preopercle, preceded by a thickening representing pterygiophores of first six dorsal rays of juveniles. First fin rays short, succeeding rays becoming rapidly longer to about point of maximum body depth, height of fin then increasing more slowly, with longest rays slightly before anus. Behind level of anus fin rays become

TABLE 1.—Regression parameters for selected morphometric characters in *Desmodema*; p = *polystictum*, l = *lorum*.

Characters	Species	Intercept	Slope	Correlation coefficient	*N*
SV vs. SL[1]	p	40.7	0.30	0.97	11
	l	54.8	0.19	0.97	8
HL[2] vs. SV	p	−1.95	0.29	0.95	15
	l	−1.02	0.28	0.98	15
Depth at pelvics vs. SV	p	8.72	0.30	0.97	15
	l	14.57	0.28	0.96	15
Greatest depth vs. SV	p	6.93	0.35	0.97	15
	l	10.66	0.35	0.97	14
Depth at anus vs. SV	p	−0.39	0.20	0.92	15
	l	5.16	0.20	0.97	15
Depth at caudal base vs. HL	p	−0.13	0.02	0.95	11
	l	0.65	0.03	0.78	8
Orbit diameter vs. HL	p	0.05	0.40	0.97	14
	l	0.09	0.36	0.98	15
Eye length vs. HL	p	−0.52	0.38	0.96	14
	l	−0.46	0.33	0.99	14
Snout vs. HL	p	−1.19	0.38	0.99	15
	l	−1.50	0.42	0.93	15
Maxillary length vs. HL	p	0.65	0.37	0.99	15
	l	0.44	0.38	0.99	15
Maxillary width vs. HL	p	−2.27	0.34	0.96	15
	l	−2.81	0.34	0.96	15
Interorbit vs. HL	p	0.31	0.23	0.96	13
	l	−0.56	0.26	0.71	15
Pectoral-pelvic origin vs. HL	p	4.10	0.25	0.97	15
	l	8.07	0.23	0.75	14
Pectoral length vs. HL	p	4.26	0.32	0.95	12
	l	6.69	0.21	0.97	8
Longest dorsal ray vs. HL	p	19.66	0.31	0.81	11
	l	2.90	0.88	0.94	12

[1]SV = Snout vent length, SL = Standard length.
[2]HL = Head length.

TABLE 2.—Caudal and pectoral rays in *Desmodema*.

Species	Caudal rays 4	5	6	7	8	9	10	$\bar{x}$
D. polystictum				5	8	1	1	7.9
D. lorum	1	1	9	1				5.8

Species	Total pectoral rays 23	24	25	26	27	$\bar{x}$
D. polystictum		5	3	6	2	25.3
D. lorum	2	7	2	3		24.4

rapidly shorter, then fin margin even to caudal base. Pelvics absent but with buried bases still evident. Pectorals low, their bases almost horizontal, outline pointed, tip probably extending almost to lateral line when fin is intact.

Color in alcohol dark brown. Dorsal fin clear, becoming dusky, then black along tail. Caudal black. Pectoral clear. Iris dark, with a golden ring around pupil. In life the fish is silvery with dark red tones dorsally and on the head, and the fins red, except that the dorsal rays along the tail extension are black.

Description of prejuvenile.—Ventral profile of body sloping gradually down from tip of lower jaw to pelvic, then tapering in a gentle curve back to beginning of narrow tail section. Vent asymmetrical, opening on left side. Dorsal profile of head steep, but less so than in *D. lorum* of the same size. In the 44-mm SV individual, the profile is almost vertical to the dorsal origin, but in larger juveniles the slope is gentler, and slightly rounded above the eyes.

Dorsal profile of body curved from dorsal origin to over opercle then tapering back to tail. Point of maximum body depth just behind pelvic bases. Tail extension thin, but relatively short; postanal length about one-quarter of standard length. The narrow part of the tail is characteristically curved upward, so that caudal fin points up and forward.

Head length about 4 in snout-vent length, about 1.6 in greatest body depth. Eye diameter slightly greater than snout length. Ascending processes of premaxillae end over anterior third of eye. Dorsal origin over middle of eye, first five or six dorsal rays elongate, remainder of fin much as in adults.

Pelvic fins present, close together, origin level

TABLE 3.—Vertebral counts in *Desmodema*.

Species	Precaudal 18	19	20	21	22	23	24	25	$\bar{x}$
D. polystictum	1	3	3						19.3
D. lorum				2	6	9	2	2	22.8

Species	Preanal 37	38	39	40	41	42 . . .	46	47	48	49	50	51	$\bar{x}$
D. polystictum	1	3	1	1	—	1							38.5
D. lorum							3	5	—	5	3	1	48.2

Species	Total 71	72	73	74 . . .	106	107	108	109	110	$\bar{x}$
D. polystictum	4	2	—	1						71.7
D. lorum					2	—	2	2	2	108.5

with rear end of pectoral base. Orientation of fin bases and shape of rays as described for *D. lorum*. Pelvics frayed in all specimens, but reaching beyond end of caudal in one and to caudal base in another.

Color in alcohol pale, with a dusky area above and behind head, extending over forehead and anterior to snout tip. Ventral parts of head dusky, a dark streak below eye, running down behind maxilla, a dusky streak along throat to pelvic base. Body with conspicuous black spots which are somewhat larger and more widely spaced posteriorly and above midline. No spots conspicuously larger than others. A narrow dark streak on back along dorsal base, running out to caudal base. Probable life colors, based on two frozen specimens, silver with black spots; iris silver and the dorsal and caudal red; pectorals with pink tinge. This coloration corresponds well with that of the figure given by Tanaka (1908) except that the iris is shown by him as green. Smaller individuals differ (our smallest 32 mm SV) mainly in that the body is less deep and the ventral profile nearly straight, and there are no polka dots. The 37.5-mm SV holotype of *T. deltoideus* was described as "uniform bright silvery." A 55-mm SL individual in poor condition has traces of spots.

Remarks.—Leapley (1953) figured and described a Florida specimen of *D. polystictum* under the name *Trachipterus trachyurus* Poey 1861. The identification was based on the presence of 76 dorsal rays in Leapley's specimen, Poey's specimen having been reported to have 82 dorsal rays.

Leapley's photograph is of a *Desmodema* with a large eye and a relatively deep tail, in agreement with *D. polystictum*. No vertebral counts were given, but Frank Schwartz (pers. commun.) has supplied vertebral counts for Leapley's specimens, as well as an additional individual from the western North Atlantic. Both have 18 precaudal vertebrae, also in agreement with *D. polystictum*.

If Leapley's identification were correct, Poey's name would be a senior synonym of *Desmodema polystictum* (Ogilby 1897). However, three characters indicate that *D. polystictum* cannot be identified with *T. trachyurus*. These are number of ventral rays (6 in *trachyurus*, 8 or 9 in *polystictum*), pectoral rays (15, vs. 12-14), and coloration (silvery with a midlateral yellow band vs. polka-dotted). In addition, *T. trachyurus* was described as having vertebral processes piercing the skin (probably an artifact caused by postmortem drying) and lacking elongated anterior dorsal rays (present in all juvenile trachipterids).

The supposed agreement in low number of dorsal rays is invalid, since Leapley's specimen was broken far in advance of the caudal. Using his value for body depth of his specimen (141 mm) we estimate the actual length to have been between 1,400 and 1,500 mm. Poey's description does not allow the identification of *T. trachyurus* with any known trachipterid. *Zu cristatus* is excluded because juveniles of that form are strongly barred and have peculiar fleshy abdominal lobes that are unlikely to go unmentioned in a description.

The species of *Trachipterus* are not completely understood, but juveniles of that genus have dark markings, a dorsal pennant, and tubercles along the venter.

Material examined.—Western and Central Pacific: CAS SU 23783, Sagami Bay 1(72.8, 102.5); CAS 5532, Rurutu, Tubuai Islands 1(37.5, 49.9), holotype of *Trachipterus deltiodeus*. Eastern Pacific: UCLA W58-103, 96 km southwest of Cabo San Lucas, Baja California, tuna purse seine, 2(66, 91 and 88, 125); SIO 70-142, 19°50′N, 106°15′W, tuna purse seine, 1(260); SIO 68-33, 19°53′N, 110°46′W, "5 × 5" nekton net towed at 5 knots, 800 m wire out, 1(333, 1,040); SIO 63-915, 16°01.5′N, 100°54′W, "5 × 5" nekton net, 0-200 m, 1(277, 785); SIO 76-167, 12°55′N, 90°54′W, tuna purse seine, 1(111.5); SIO 76-294, 12°35′N, 92°15′W, tuna purse seine, 1(84.9, 126.5); SIO 76-67, 12°15′N, 92°25′W, tuna purse seine, 1(42); UCLA W67-135, 11°48′N, 88°25′W, 1(60 SL); SIO 73-392, 11°18′N, 91°31′W, tuna purse seine, 1(91.5); SIO 75-139, 10°00′N, 119°00′W, midwater trawl, 0-50 m, 2(74.3, 100.5 and 90 SL); SIO 76-325, 10°24′N, 107°46′W, midwater trawl, 225 m wire out, 1(25.5); SIO 73-400, 08°41′N, 85°03′W, dipnetted at surface, 1(82); SIO 64-397, 03°18.4′N, 101°54.3′W, stomach of *Alepisaurus ferox* 1(55.5); SIO 63-299, 04°03′N, 80°46′W, meter net, 400 m wire out, 1(23); SIO 75-590, 00°00.2′S, 119°17.0′W, meter net, 0-200 m, 1(28.0, 36.0); SIO 52-334, 02°47′S, 112°13′W, meter net, 0-250 m, 1(29, 40.5); SIO 73-340 "Eastern N. Pacific," tuna purse seine, 1(296, 835).

Desmodema lorum n.sp.

Figures 3, 4, 5, 6

Desmodema polysticta, not of Ogilby. Fitch

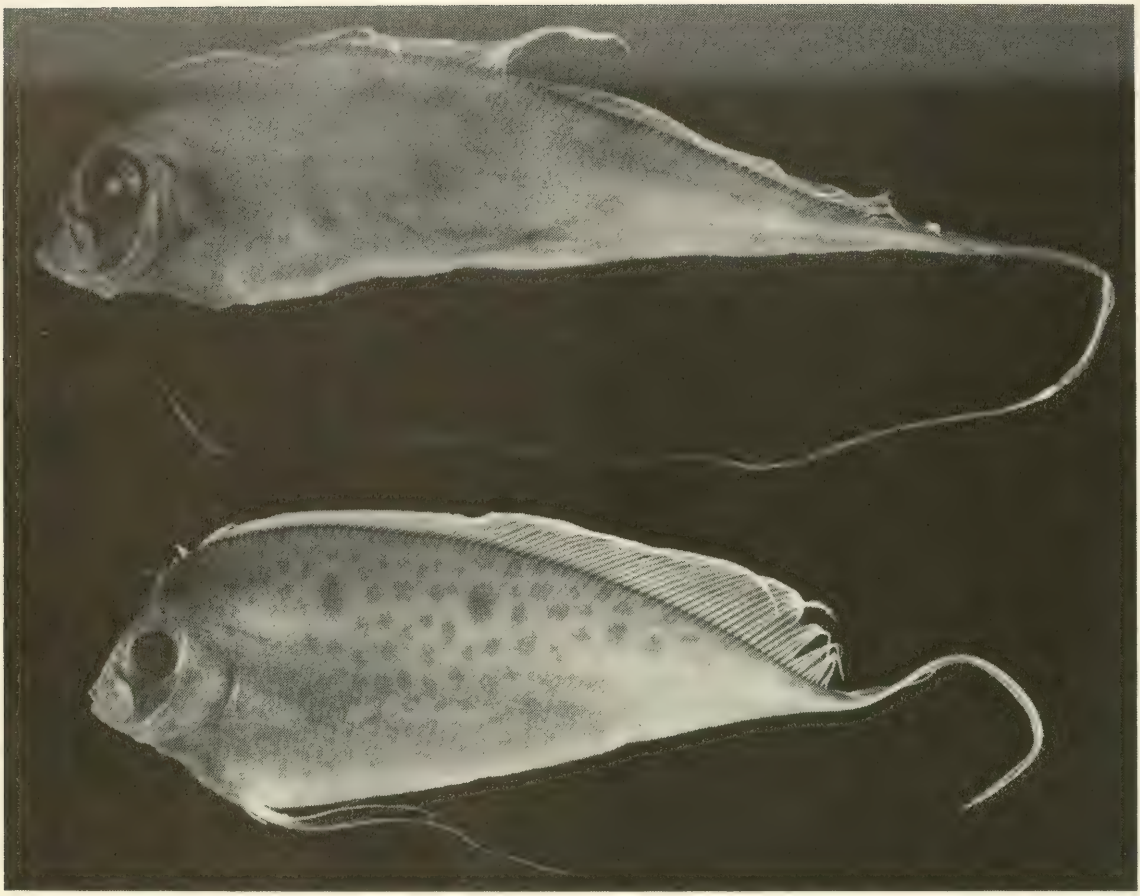

FIGURE 5.—Juvenile and prejuvenile of *Desmodema lorum*. Upper figure juvenile, LACM 35237-1, 103.7 SV, 412 mm SL. Lower figure prejuvenile, LACM 30230-1, 95 mm SV, 198 mm SL.

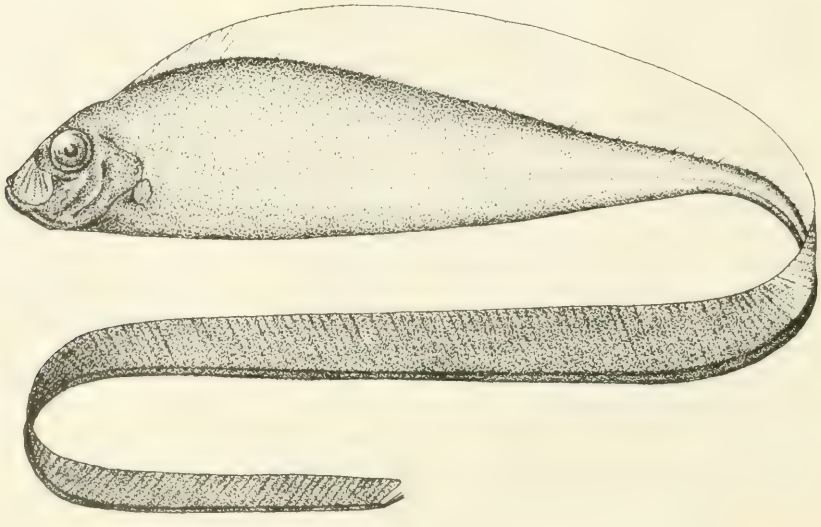

FIGURE 6.—Holotype of *Desmodema lorum*, USNM 216726. Fins reconstructed.

1964:321; in part, all but 10th, 12th, 13th of listed specimens (fig. 2 is *D. lorum*, fig. 3 is *D. polystictum*).

Desmodema polystictum, not of Ogilby. Berry and Perkins 1966:668. Fitch and Lavenberg 1968:88. Miller and Lea 1972:87.

Desmodema polystictus, not of Ogilby. Radovich 1961:18.

Diagnosis.—A *Desmodema* with 106-111 total vertebrae (21-25 precaudal and 46-50 before the anus), 4-7 (usually 6) caudal rays, snout length greater than eye diameter, an exceedingly long attenuate tail in juveniles and adults (Figures 3, 7) and scales present in prejuveniles and small juveniles.

Description of adult (see also Tables 1-3).—Ventral profile of body almost straight, but with a slight convexity back to anus, then tapering back to elongate tail section. Dorsal profile rising rapidly from snout tip to dorsal origin, then ascending more gently to maximum depth of body about one-half to three-quarters of head length behind head, then tapering back to tail. Tail exceedingly long and narrow, postanal length three-quarters of standard length. Anus on ventral midline.

Head length 3.2-3.8 in snout-vent length, 1.2-1.3 in greatest body depth. Eye moderate, equal to or (usually) shorter than snout. Ascending processes of premaxillae ending over or behind rear margin of eye. Dorsal origin just behind preopercle to over middle of opercle, preceded by a horny process representing pterygiophores of first six dorsal rays. First few dorsal rays short, succeeding rays becoming longer, with maximum height of fin over and posterior to anus. Fin height decreases gradually along tail, probably as reconstructed in Figure 6. Pelvics absent, but with buried bases still evident. Pectorals low, their bases horizontal. Pectoral pointed, but tip frayed and broken in all specimens.

Color in alcohol tan. Dorsal fin clear, becoming dusky, then black along tail. Caudal black. Pectorals clear. Iris dark with a golden ring around pupil. In life, probably silvery with red tones dorsally and on the head, and with the fins red.

Description of prejuvenile.—Ventral profile sloping down from tip of lower jaw to pelvics, then tapering convexly back to vent, then tapering more sharply to beginning of tail, then straight.

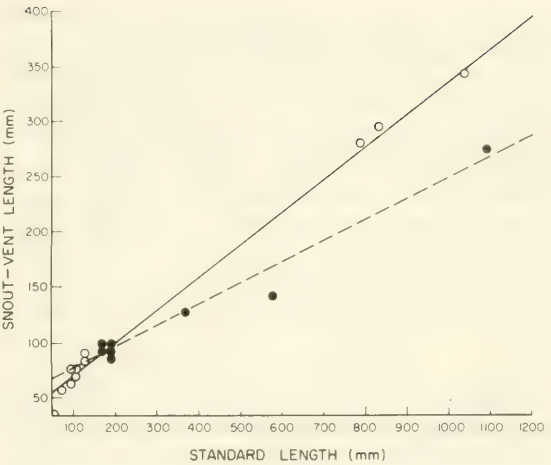

FIGURE 7.—The regression of snout-vent length on standard length in *Desmodema*. Open circles *D. polystictum*, closed circles *D. lorum*.

Usually a notch in outline at position of vent, which is asymmetrical, opening on the left side. Dorsal profile of head steep, almost vertical in smaller specimens. Back curved, point of maximum body depth just behind pelvic base. Dorsal profile becomes straight along tail elongation. Tail long and thin, postanal length about one-half of standard length.

Head length 3.8-4.2 in snout-vent length, 1.8-2.2 in greatest body depth. Eye about equal to snout length. Because of the steepness of the forehead, the ascending processes of the premaxillae end over the anterior third of the eye.

Dorsal origin over middle to posterior third of eye. First five or six dorsal rays elongate, remainder of fin shaped much as in adult except that the rays along the elongate tail are not as long. Pelvic fins present, close together, origin under pectoral base. Anteroposterior axes of pelvics parallel with sides. Pelvics broken in all our material, but reaching beyond anus in one specimen. Pelvic rays flattened and bladelike basally, the first the broadest, becoming filamentous distally. Minute prickles along rays. Pectorals as in adults.

Color in alcohol tan, a darker area on back over and behind head, extending down over forehead onto snout. A variably developed dusky streak from lower margin of orbit down behind maxilla. A dusky streak along throat to pelvic bases. Spotting somewhat variable but spots becoming larger and more widely spaced posteriorly and above midline. Three of five specimens with two noticeably larger

spots on upper back on middle-third of body (see Figure 4). A narrow dark streak on back at base of dorsal, broadening on narrow part of tail. Individuals of about 35 mm SV differ in that the body is not so deep, and there is little or no pigment. Also the dorsal is relatively higher. Our smallest specimen, 18.5 mm SV, has the back with a straight taper behind the head, the ventral profile more evenly tapering, and has scattered melanophores on the head and over the viscera. These probably represent the larval pigmentation.

Identification and remarks.—The characters given in the generic and specific diagnoses serve to distinguish *D. lorum* adequately from all known trachipterids. In addition to the characters given in the diagnoses, the two species of *Desmodema* differ in number of dorsal rays. The single *D. lorum* counted had 197 dorsal rays and three *D. polystictum* had 120, 124, and 121, respectively. Another feature is the height of the dorsal. Large *D. lorum* have proportionately longer dorsal rays than do *D. polystictum* of equivalent size (Figure 8, Table 1). Prejuveniles of *D. lorum* can most easily be distinguished from those of *D. polystictum* by their deeper body, and more rounded anteroventral contour (Figure 4).

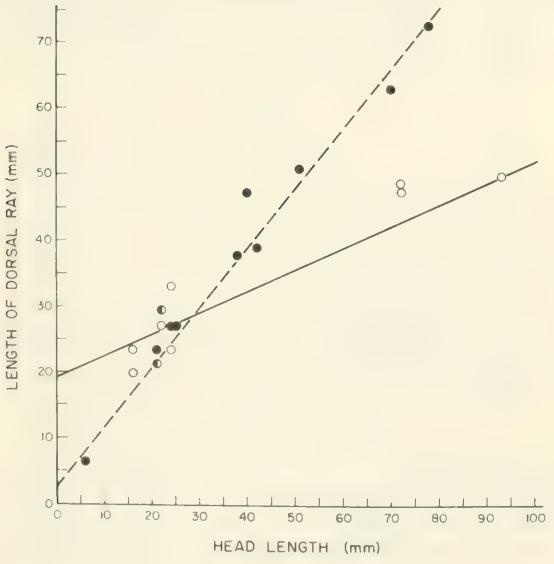

FIGURE 8.—The regression of length of longest dorsal ray on head length in *Desmodema*. Open circles *D. polystictum*, closed circles *D. lorum*.

Although Ogilby did not illustrate the holotype of *Trachypterus jacksoniensis polystictus*, his description is sufficiently detailed to allow identification with considerable certainty. The polka-dotted coloration and lack of lower caudal lobe are diagnostic of *Desmodema*, and the dorsal ray count of 126 indicates that our material has been correctly assigned. The caudal count of seven or eight rays also accords with our concept of *D. polystictum*. Tanaka's (1908) excellent figure indicates that *Trachypterus misakiensis* has properly been synonymized with *D. polystictum*, and the presence of eight caudal rays in the small holotype of *Trachipterus deltoideus* dictates a similar placement.

Etymology.—From the Latin *lorum*, a whip, in reference to the elongate tail. Suggested common name, whiptail ribbonfish.

Material examined.—Holotype: USNM 216726, formerly SIO 62-434, a 1,098 mm SL (276 mm SV) male, taken between 29°05′N, 126°37′W and 29°03′N, 126°42′W by RV *John N. Cobb* with a Cobb Mk II trawl with 1,200 m wire out (estimated fishing depth 400 m) between 1930 and 2110 h on 25 August 1962. (Original station number 90.160, C6208, see Berry and Perkins 1966.) Paratypes: LACM 30217-1, 34°42′N, 121°20′W, spit up by *Thunnus alalunga*, 1(91.5, 167); LACM 9890-2, 34°25′N, 120°28′W, 15.2-m midwater trawl, 8 fm, 1(97, 173); LACM 9982, 33°00′N, 118°03′W, IKMT, 2,743 m wire out, 1(131); SIO 76-335, 13 km west of Oceanside, Calif., bait net, 1(95, 198); LACM 30597-1, 32°48′N, 118°16′W to 32°30′N, 118°30′W, IKMT, 1(87, 188); LACM 35237-1, 32°43′N, 118°57.5′W, 10-m midwater trawl, 1(103.7, 412); LACM 31678-1, San Clemente Island, Calif., off Pyramid Head, 1(83); LACM 30998-1, 31°45′N, 118°48′W to 31°44′N, 118°00′W, IKMT, 1,300 m, 1(93); SIO 63-375, 31°40.5′N, 122°03.5′W to 31°37.0′N, 122°04.3′W, Cobb Mk II trawl, 1,144 m wire out, 1(139.8, 580); SIO 63-429, 29°58.5′N, 120°07′W, IKMT, 4,500 m wire out, 1(173); LACM 9726-8, 29°29′N, 118°35′W, IKMT, 2,134 m wire out, 1(92.5, 189); SIO 74-47, 28°10.2′N, 160°00.9′E, IKMT, 0-1,000 m, 1(125, 364); UCLA W61-125, 64 km off Cabo Colnett, Baja California, 1(286), LACM 31800-2, 129 km south of Cabo San Lucas, Baja California, 1(283).

Additional material.—UCLA W55-320,

33°39′N, 135°00′W, 1; SIO 75-588, 29°17′N, 116°59′W, 1(55); UCLA A343, 28°N, 132°W, 1; UCLA W62-73, 32°10′N, 118°24′W, 1(53); SIO 75-589, 28°37.5′N, 118°18′W, 1(18.5); SIO 75-591, 33°34′N, 118°34′W, 1(89+ SL); LACM 31804, no data, 1(132); SIO 64-96, 31°39′N, 117°51′W, 1(289); SIO 72-16, 27°22′N, 155°23′W, 1(19.8, 26.4).

ACKNOWLEDGMENTS

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OXYCLINE CHARACTERISTICS AND SKIPJACK TUNA DISTRIBUTION IN THE SOUTHEASTERN TROPICAL ATLANTIC

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ABSTRACT

A shallow layer of low oxygen concentration, containing minimum values frequently less than 1.0 ml/l and a strong oxycline, was measured on two cooperative cruises in the southeastern tropical Atlantic Ocean and found to be consistent with previous portrayals and hypotheses based on fragmentary data. The low-oxygen layer was in the form of a thick wedge off the southwestern coast of Africa, extending from about lat. 18° to 3° S. The oxycline overlying the low-oxygen layer was generally coincident with a pycnocline and was found at depths of 20-50 m in most of the area surveyed, as revealed by the topography of the 3.5 ml/l iso-oxygen surface. It is believed that a shallow oxycline has a strong influence on the distribution and availability of skipjack tuna schools. The hypothesis was tested by overlaying school sighting positions on the 3.5 ml/l topography. The association between sightings and oxycline depth was further defined by developing a linear "equation" relating the two variables as follows: $s = 23.15 - 0.59z$, where s is the number of school sightings, z is the depth of the 3.5 ml/l surface, and 23.15 and 0.59 are constants. A similar correlation was attempted with school sightings and habitat layer thickness, but the results were less systematic and convincing than the oxycline correlation.

A shallow oxycline containing low values of dissolved oxygen concentration should serve as a lower boundary of the environment habitable by surface schooling tunas. In a study of the relationship of thermocline depth to success of purse seining of tuna in the tropical Pacific, Green (1967) stated that an oxycline approximately coincident with the thermocline could play a major role in restricting the fish to near surface waters. Work on the oxygen requirements of captive skipjack tuna in the Southwest Fisheries Center Honolulu Laboratory[3] by R. M. Gooding and W. H. Neill indicated a 4-h TL_m (median tolerance limit) between 2.4 and 2.8 ml O_2/l, and in experiments with gradually declining oxygen concentrations an alarm threshold was found near 3.5 ml/l. If we regard the 3.5 ml/l iso-oxygen surface to be the "floor" of habitable environment of surface schooling tunas in tropical waters, then the topography of this surface becomes significant in describing their environment.

The shoaling of the oxycline, the floor of the habitable environment, may serve not only to crowd the skipjack tuna schools to the surface, but also to influence the lateral distribution of the fish schools through other ecological factors associated with the shoaling. The oxycline is imbedded in the thermocline, which is brought up to or near the sea surface under conditions of upwelling which seasonally occur off the southwestern coast of Africa. Such conditions, when well developed, will lead to the development of fronts, which tend to concentrate forage, and higher rates of primary and secondary productivity to sustain larger forage populations; both processes tending to concentrate predators such as tunas, as described by Blackburn (1965).

BACKGROUND INFORMATION ON OXYGEN MINIMA IN THE SOUTHEASTERN ATLANTIC

The oxygen minima in the Atlantic have been studied since the early part of this century. These studies have not, however, resulted in a definitive explanation of the mechanisms of formation of these low-oxygen layers. While many theories have been proposed to explain the origin of these layers, the mechanisms generally cited as being most significant are either an extremely high biochemical oxygen consumption or low rates of oxygen replenishment by mixing processes. Some recent papers have dealt with a synthesis of these

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[3]Neill, W. H. Unpubl. exp. data, Southwest Fish. Cen. Honolulu Lab., Natl Mar. Fish, Serv., NOAA, pers commun., 1974 and 1976.

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processes in an attempt to give a more complete explanation of the observed patterns (Wyrtki 1962; Bubnov 1966, 1972; Menzel and Ryther 1968).

Proponents of the first mechanism argue that an oxygen minimum layer is formed as a result of biochemical oxidation of organic matter that has accumulated at intermediate depths due to specific gravity relationships between seawater and sinking detritus (Seiwell 1937; Miyake and Saruhashi 1956). Those supporting the second mechanism suggest that an oxygen minimum will be formed at the relatively still boundary between circulating water masses where replenishment of oxygen will be minimal. This view was first advanced by Jacobsen in 1916 and was later supported by Dietrich and Wüst (Richards 1957).

More recent studies (Redfield 1942; Wyrtki 1962; Bubnov 1966, 1972; Menzel and Ryther 1968) have stressed the importance of advective processes in the formation of oxygen minimum surfaces. Redfield (1942) hypothesized that the deep oxygen minimum of the Atlantic could be formed by advection along isentropic surfaces of water carrying a heavy load of organic detritus and solutes from high latitude convergence areas. Subsequent oxidation of the organic load forms a minimum. Wyrtki (1962), Menzel and Ryther (1968), and Bubnov (1966, 1972) considered high oxygen consumption as necessary for initial formation of low-oxygen water with advective and mixing processes controlling its position and movement. Wyrtki (1962) contended that oxidation occurring in the layer of least advection results in formation of an oxygen minimum, which can spread by mixing into other water masses. Menzel and Ryther (1968) and Bubnov (1966, 1972) argued that oxygen depleted water will form in specific areas due to high biochemical oxygen consumption and that these waters are then spread by advection and turbulent diffusion.

Bubnov (1972) stated that the main factors controlling the formation of an oxygen minimum are the rate of biochemical oxidation, the density stratification of the water, and the supply of oxygenated water to bottom layers. In the southeastern tropical Atlantic the presence of one or more of these factors results in highly favorable conditions for the formation of an oxygen minimum. The coastal region off South-West Africa has strong upwelling conditions which result in high organic production and subsequent high oxygen consumption (Hart and Currie 1960). Though the coastal waters are weakly stratified in comparison with the region of the Congo River effluent, there is, nonetheless, a well-developed pycnocline which inhibits downward-mixing of highly oxygenated surface waters (Visser 1970; Bubnov 1972). In addition, the deep waters of the Angola Basin are somewhat lower in oxygen than those of the western basin of the South Atlantic. This reduces the amount of oxygen which will be mixed into the upper layers by upwelling or turbulent diffusion (Bubnov 1972). Taft (1963) and Visser (1970) suggested that the waters to the north of lat. 20°S off the coast of South-West Africa may be isolated from the highly oxygenated deepwater masses formed at high latitudes, thus inhibiting the renewal of oxygen from this source.

Because of the favorable conditions for the formation of low-oxygen water in the coastal region of South-West Africa, it has been suggested that this area is a source for much of the water that forms the oxygen minimum surfaces in the South Atlantic. Taft (1963) plotted the oxygen and salinity distributions on surfaces of constant potential specific volume anomaly for the South Atlantic. On the 125, 100, and 80 cl/t surfaces ($\sigma\theta$ 26.81, 27.07, and 27.49 g/l, respectively), the isopleths of both oxygen and salinity are zonal at lat. 20°S. The areas of lowest oxygen concentration are located just north of lat. 20°S off the coast of South-West Africa, strongly suggesting that this region serves as a source area for low-oxygen water which is then transported westward to form the primary minimum at 300-600 m in the study area).

In a study by Menzel and Ryther (1968), the concentration of dissolved organic carbon in the South Atlantic was found to be essentially constant below 400-500 m while the oxygen content varied. Based on this finding, they concluded that oxygen concentrations in the minimum layer will not be further reduced by in situ decomposition of organic matter. They suggest that low-oxygen water is formed off South-West Africa and is then distributed horizontally along isentropic surfaces to form the primary oxygen minimum layer. Changes in the oxygen content occur by mixing with water masses of higher oxygen content, resulting in the increase of oxygen concentrations as the water moves farther from its source.

Bubnov (1972) identified three areas off South-West Africa where waters of very low oxygen content are formed (see Figure 1): 1) the shelf region to the south of lat. 17°S, 2) the coastal

region extending from long. 8°-10°E to the shelf, and from lat. 7°-9°S to 17°-18°S, and 3) the region of the quasi-stationary cyclonic gyre to the west of long. 6°E.

In the shelf region south of lat. 17°S, water with extremely low-oxygen content (<1 ml/l) forms in the near-bottom layer (80-150 m) and spreads northward and westward beneath the warmer, less dense surface water by advection and turbulent diffusion. This water forms the shallow minimum layer that is characteristic of this region, extending westward to about long. 0° where it loses its identity due to mixing.

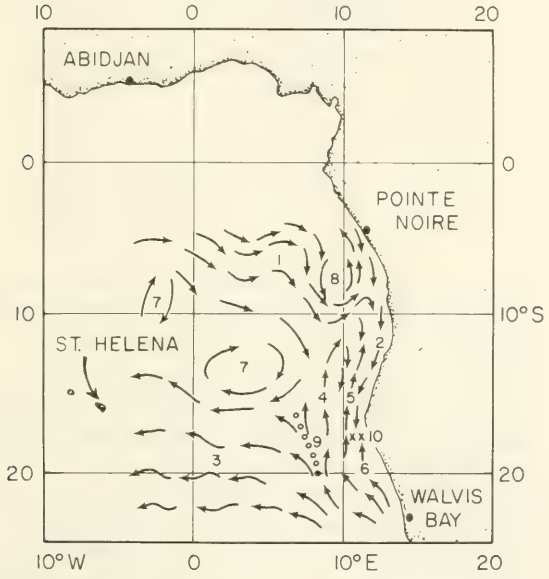

FIGURE 1.—Diagram of geostrophic water circulation in the 0 to 100 m layer. 1) South equatorial countercurrent; 2) Angola Current; 3) west (main) branch of Benguela Current; 4, 5, 6) north branches of Benguela Current; 7) eddies in inner region of cyclonic gyre; 8) anticyclonic curl; 9) Benguela divergence; 10) merging zone of Angola Current and north littoral branch of Benguela Current. From Moroshkin et al. (1970).

The "eastern coastal region" and the region of the cyclonic gyre are areas where low-oxygen water (<1 ml/l) forms at "intermediate" depths (Bubnov 1972). These waters apparently are advected and mixed to the west, forming the primary oxygen minimum in the eastern South Atlantic. These observations provide further evidence to support the hypothesis that the coastal waters off Southwestern Africa are a source for much of the low-oxygen water that forms the oxygen minima in the South Atlantic.

RESULTS OF JISETA CRUISES

In 1968 the National Marine Fisheries Service, then Bureau of Commercial Fisheries, joined with the U.S. Coast Guard and the Missao de Estudos Bioceanologicos e de Pescas de Angola in the Joint Investigation of the Southeastern Tropical Atlantic (JISETA); an oceanographic and biological investigation in the coastal waters of southwestern Africa. Distribution of tunas and oceanographic conditions from the Equator to lat. 18°S were investigated on cooperative cruises of the RV *Undaunted*, the USCGC *Rockaway*, and the RV *Goa* during February through April and September through December 1968.

Low-Oxygen Layer

Vertical sections of dissolved oxygen concentration developed from the JISETA data (Cook et al. 1974) characteristically showed a layer of low oxygen concentration, including a minimum which frequently was <1.0 ml/l and occasionally <0.5 ml/l in concentration. The minimum values were not well defined because of the means of sampling employed: 1 cast of 10 Niskin bottles spaced throughout the upper 1,000 m of the water column at each station. However, the samples were spaced well enough to portray the layer of low concentration and the sharp oxycline which formed its upper boundary.

The transects obtained in March 1968 (Figures 2, 3) showed a layer of oxygen concentration <1.0 ml/l of variable thickness (50-450 m) extending from lat. 15° to 18°S in the upper 500 m of the water column. In the southern portion of the area the layer was thicker and nearer the sea surface.

In the October-November transects (Figures 4, 5) a thick layer of water containing <1.0 ml/l dissolved oxygen was found to extend from lat. 17° to 7°S in the upper 600 m of the water column. Once again the layer was thicker (up to 550 m) and nearer the surface in the southern portion of the area. In the northern portion it thinned to <100 m and was detected at about 300-400 m depth at the outer stations, about n.mi. (180 km) offshore.

The form of the layer of very low oxygen concentration (<1.0 ml/l) observed in October-November 1968 (Figure 6) appears to be consistent with Bubnov's (1972) contention that the source of the layer is located in coastal waters between lat. 18° and 23°S, from which it is advected northward by the northern branches of the Benguela Cur-

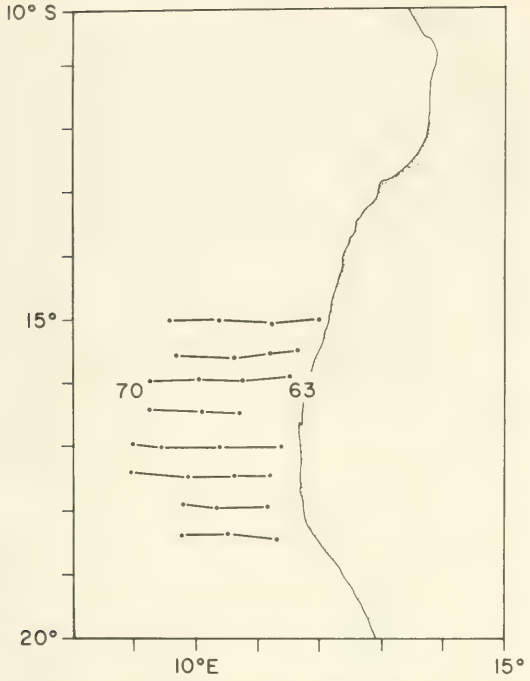

FIGURE 2.—Locations of transects of dissolved oxygen concentration conducted by *Undaunted* during 8-16 March 1968. From Cook et al. 1974.

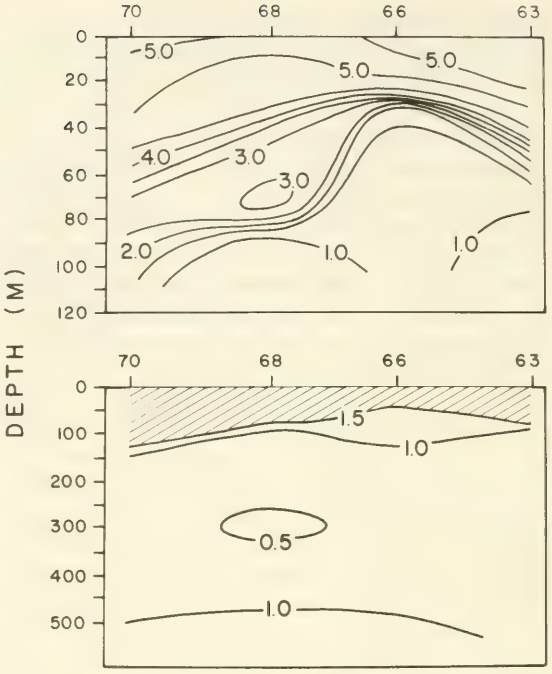

FIGURE 3.—One of the transects of dissolved oxygen concentration (milliliters per liter) produced from *Undaunted* data (8-16 March 1968). From Cook et al. 1974.

rent. The apparent divergence of the layer from the coast shown in the onshore-offshore transects north of lat. 9°S (Cook et al. 1974) also is consistent with the general direction of flow given for the extension of the current.

Although a subsurface oxygen minimum was found throughout the area surveyed from lat. 18°S to the Equator, the layer of very low oxygen concentrations (≤1.0 ml/l) extended northward only as far as lat. 7°-8°S. The increase in oxygen concentration northward from those latitudes is the result of either westward turning of the northward currents carrying the low oxygen concentrations as suggested by Bubnov (1972) or increased mixing rates attenuating the oxygen minimum.

Oxycline

Overlying the layer of low oxygen concentration throughout its extent was an intense oxycline. The range of concentrations in the oxycline usually was from 2.0 to 4.0 ml/l, but was found to be as great as from 1.0 to 5.0 ml/l in the southern portion of the surveyed area. The oxycline thickness ranged from about 40 m to 10 m, producing intense vertical gradients when thinnest. The most intense gradients were found on the shoreward ends of the transects and in the southern portion of the surveyed area.

The 3.5 ml/l iso-surface was selected to portray oxycline topography because it was found in the upper oxycline throughout the area surveyed (lat. 18°S-Equator) and because this oxygen concentration has been found to be significant in the physiology and distribution of skipjack tuna in the eastern tropical Pacific (Neill see footnote 3; Barkley et al.[4]). The resulting topographies for the February-April and October-November periods (Figures 7, 8) were generally of low relief and shallow (≤50 m) except at the seaward end of transects south of lat. 16° S in March and north of lat. 2°-3° S in October-November. Two large areas of shallow depths (≤25 m) to the oxycline were found in the October-November data field, from lat. 10° to 16°S and from lat. 5° to 7°S. Due to the

[4]Barkley, R. A., W. H. Neill, and R. M. Gooding. 1977. Skipjack tuna habitat based on temperature and oxygen requirements. Unpubl. Manuscr. 12 p. Southwest Fish. Cen. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, P.O. Box 3830, Honolulu, HI 96812.

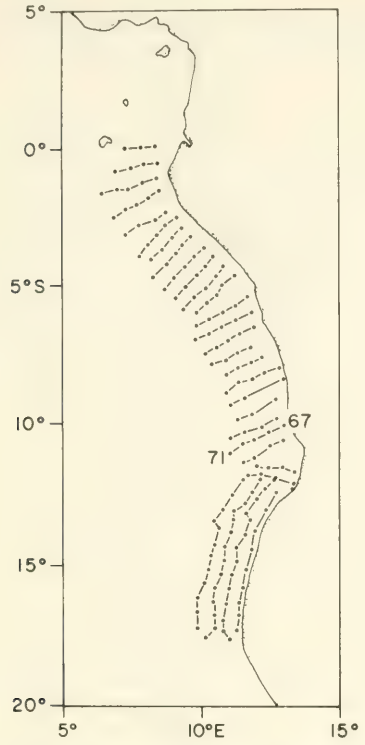

FIGURE 4.—Location of transects of dissolved oxygen concentration by *Undaunted* and *Rockaway* 15 October-21 November 1968. Derived from Cook et al. 1974.

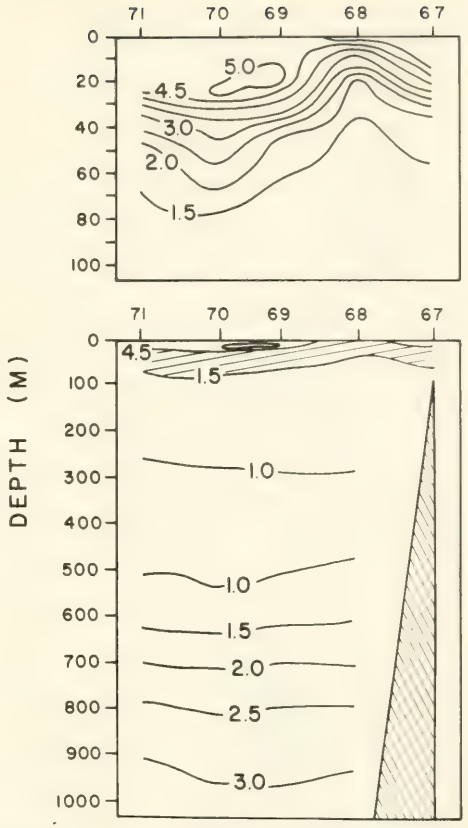

FIGURE 5.—One of the transects of dissolved oxygen concentration (milliliter per liter) produced from *Undaunted* data (22-23 October 1968). From Cook et al. 1974.

relatively incomplete sampling grid in the February-April period, little can be learned from any attempts to compare the results of the two periods.

Pycnocline

The density field of the upper waters off southwestern Africa is determined mostly by temperature, except in the area influenced by the effluent of the Congo River (Bubnov 1972). Results of the JISETA cruises support this contention, showing a well-developed thermocline throughout the area.

During the October-November period thermocline gradients increased from south to north with the most intense gradients found off the Congo River. The sea-surface temperature ranged from $<17°$ C in the south (lat. 18° S) to $>26°$ C near the Equator. In the February-April period the thermocline appeared to be more intense than during the October-November period but generally con-

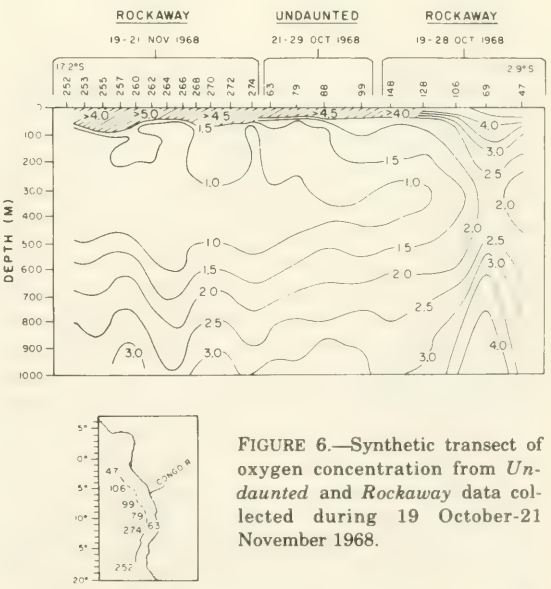

FIGURE 6.—Synthetic transect of oxygen concentration from *Undaunted* and *Rockaway* data collected during 19 October-21 November 1968.

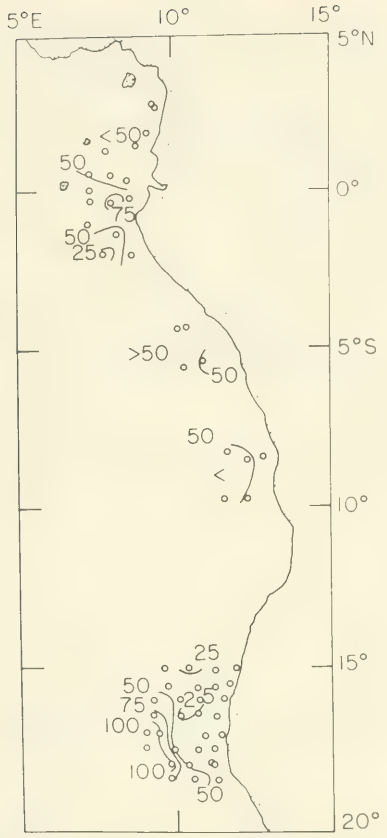

FIGURE 7.—Depth (meters) to the 3.5 ml/l iso-oxygen surface from *Undaunted* data, February-March 1968.

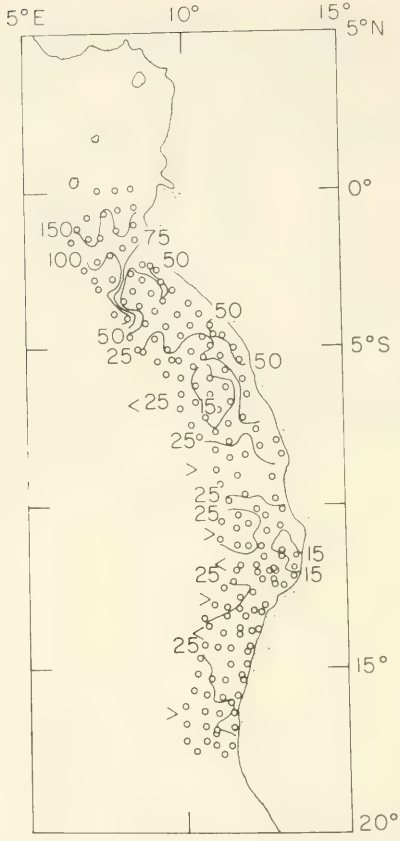

FIGURE 8.—Depth (meters) to the 3.5 ml/l iso-oxygen surface from *Undaunted* and *Rockaway* data, October-November 1968.

stant throughout the limited area surveyed. The sea-surface temperature ranged from 22°C in the south (lat. 18°S) to 29°C in the north (lat. 2°N).

In order to portray the pycnocline topography and minimize the differences in surface heating in the two periods, an isopycnal surface found near the bottom of the thermocline, the $\sigma_t = 26.0$ surface, was chosen (Figures 9, 10). Comparison of the vertical sections of density and oxygen from the JISETA cruises (Cook et al. 1974) shows that the 26.0 iso-σ_t surface parallels the oxycline and is found in its lower levels. Therefore the topography of the isopycnal surface also should reflect geostrophic circulation patterns in the lower oxycline.

During the October-November 1968 period the 26.0 g/l topography (Figure 10) deepened nearshore north of lat. 10°S, but was shallow and irregular south of there. The topography north of lat. 10°S indicates a general southward flow in the upper layer from about lat. 4° to 10°S, corresponding with the southward Angola Current described by Moroshkin et al. (1970), but not extending as far south as they portray it (Figure 1).

RELATIONSHIP BETWEEN OXYCLINE DEPTH AND SKIPJACK DISTRIBUTION

Variations in the thickness of the habitable environment of skipjack tuna, bounded beneath by the oxycline, should strongly inflence the distribution and availability of surface schooling tunas. To test this contention, the positions of sightings of skipjack schools during the October-November 1968 cruise period were plotted on a map of oxycline (3.5 ml/l) topography (Figure 11). A cursory study of this plot reveals that the fish were generally sighted where the oxycline was <50 m deep, and over 80% of the schools were seen where it was <30 m deep.

An apparent relationship between school distribution or availability and oxycline depth can

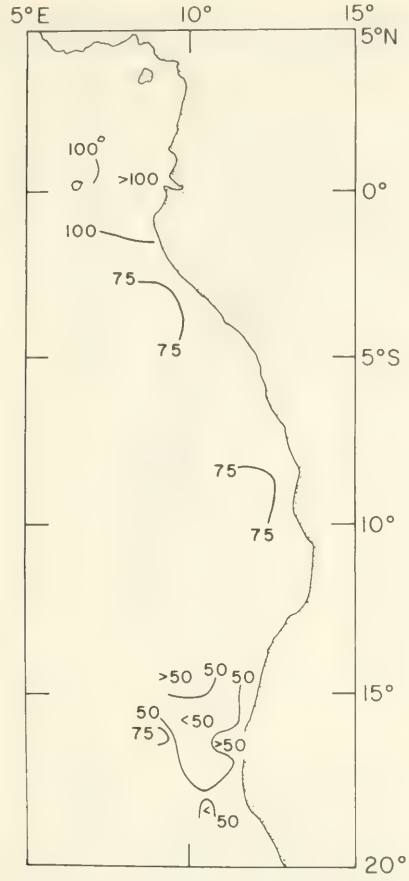

FIGURE 9.—Depth (meters) to the 26.0 g/l σ_t surface from *Undaunted* data, February-April 1968.

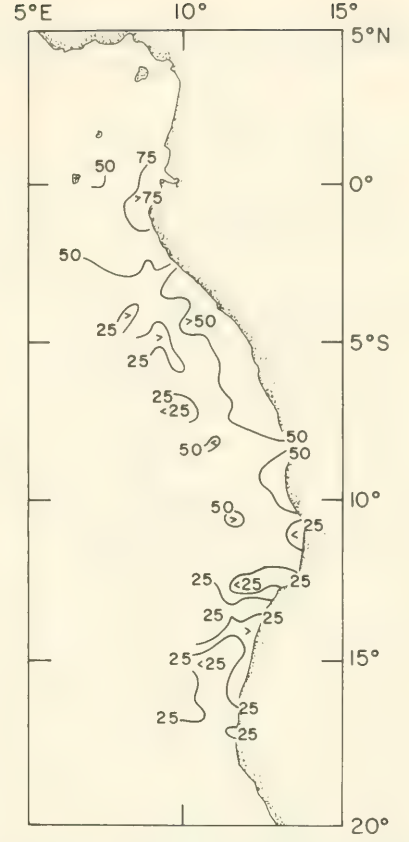

FIGURE 10.—Depth (meters) to the 26.0 g/l σ_t surface from *Undaunted* and *Rockaway* data, October-November 1968.

best be demonstrated with the data collected in October-November, involving 49 sightings with relevant oxygen data. After grouping the oxycline depth measurements into 5-m classes and plotting a sighting versus depth-frequency bar graph (Figure 12), it appears that a smooth inverse relationship exists for depths >10 m. By assigning the central value of each depth class to each sighting in the class, a least squares linear "equation" can be obtained for sighting frequency as a function of oxycline depth in the form:

$$s = a + mz \qquad (1)$$

where s = the number of sightings
z = the depth of the 3.5 ml/l surface
a and m = constants, in this case, equal to 23.15 and −0.59, respectively, leading to

$$s = 23.15 - 0.59z \qquad (2)$$

as the "equation." Note that the equation is defined only over the range of depths from 11 to 40 m. At depths greater than this, school sightings may be difficult to make and at depths less than this the fish may avoid the thin habitable layer.

Although the relationship portrayed in the bar graph appears to be nonlinear, the errors introduced by interpolation between sampling bottle depths and the arbitrary assignment of central values to the frequency classes make any attempts to obtain a best-fit, nonlinear "equation" unwarranted. The linear relationship shown above is about all the sophistication the data will bear, particularly in view of the small number of fish school sightings.

To further pursue the role of environmental conditions in influencing the distribution of skipjack tuna, we considered the concept of habit layer

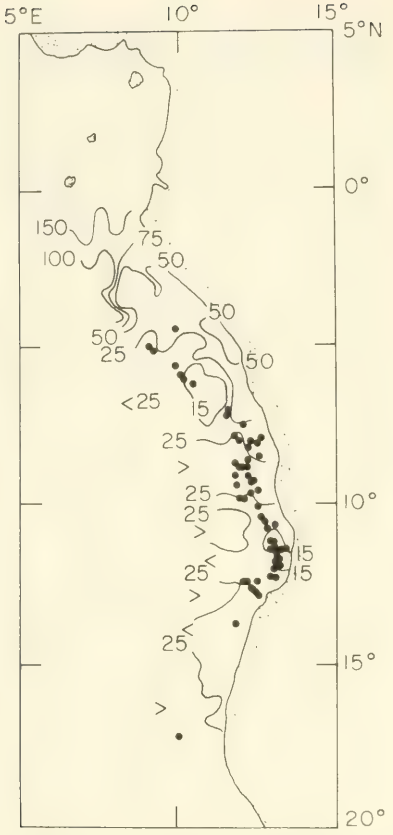

FIGURE 11.—Location of sightings of schools of skipjack tuna during October-November 1968 plotted on the observed oxycline (3.5 ml/l) topography.

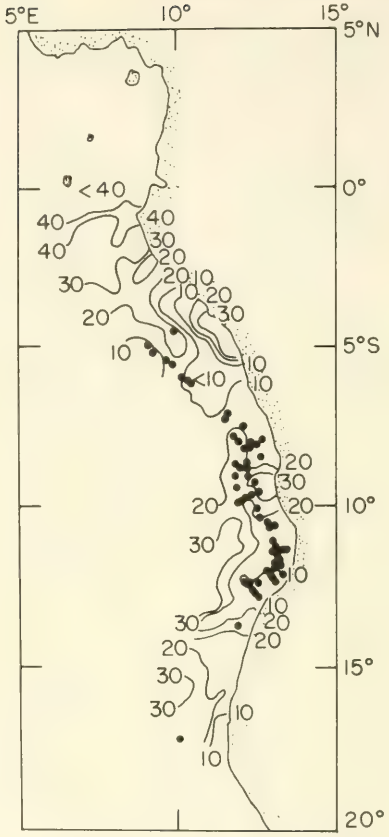

FIGURE 13.—Location of sightings of schools of skipjack tuna (dots) and habitat thickness (meters) from *Undaunted* and *Rockaway* data, October-November 1968.

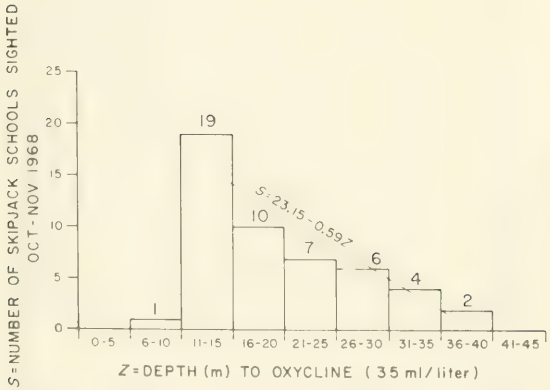

FIGURE 12.—Relationship between skipjack school sightings and oxycline depth from *Undaunted* and *Rockaway* data for October-November 1968.

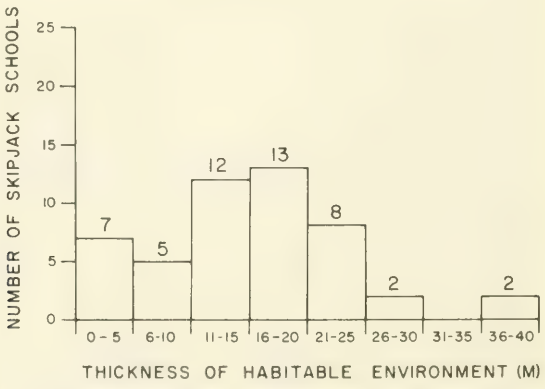

FIGURE 14.—Relationship between skipjack school sightings and habitat thickness from *Undaunted* and *Rockaway* data for October-November 1968.

developed by Barkley et al. (see footnote 4). They defined the habitat of adult skipjack to be bounded above by the sea surface or 22°-26°C (for 9- to 4-kg fish) and below by 18°C or 3.5 ml/l oxygen concentration, whichever is shallower. We plotted the skipjack tuna school sightings on a horizontal chart of habitat layer thickness (using 24°C) for the October-November cruise period (Figure 13). The distribution of school sightings at various habitat layer thicknesses (Figure 14) is considerably different from that at various oxycline depths. Many points in the school sightings versus oxycline depth plot (Figure 12) have shifted to shallower classes in the school sighting versus habitat thickness plot, including seven observations in habitat thicknesses of 5 m or less. This shift is the consequence of regarding the 18°C isothermal surface as the floor of the habitat when it is shallower than the oxycline and assuming that it has a constraining effect equal to that of the 3.5 ml/l oxygen surface. The validity of this assumption is unknown, but comparison of the two distributions (Figures 11, 13) suggest that the 3.5 ml/l oxygen surface has a stronger effect on the skipjack tuna than the 18°C isothermal surface.

The question of whether it is school distribution or availability (to a fishing method) which has been related to oxycline depth cannot be resolved without an independent assessment of tuna school distribution by a different method. The means used to locate tuna schools is essentially that employed by crews of purse seiners and live-bait boats; a watch is maintained for bird activity above feeding or "breezing" schools. This technique reveals only those schools which are available to seines or pole-and-line fishing methods, hence it would be more accurate to consider the factor portrayed in Equation (2) as availability rather than distribution. Those fish not closely approaching the surface would not be detected and would not be available to these harvesting methods.

The pragmatic significance of the relationship between skipjack tuna school availability and oxycline depth lies in its use by fishermen and fishery scientists, the former for more efficient harvest strategy and the latter for more accurate resource assessment. The coincidence of the oxycline and thermocline should provide a very strong lower barrier to downward excursions of tropical tunas, perhaps even strong enough to prevent an encircled school from escaping by sounding before the seine is pursed. If this were true, the efficiency of capture by purse seine would be greater in waters containing a shallow oxycline.

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THE SOURCE OF COBALT-60 AND MIGRATIONS OF ALBACORE OFF THE WEST COAST OF NORTH AMERICA

Cobalt is an integral part of the vitamin B_{12} complex and an important cofactor in enzyme systems (Lowman et al. 1971; Reichle et al. 1970). It is, therefore, an element whose cycle in oceanic ecosystems is of interest. The artificial radionuclide cobalt-60 (^{60}Co) has been observed in the livers of albacore, (*Thunnus alalunga* Bonnaterre) collected off the west coast of North America, Washington to Baja California (Pearcy and Osterberg 1968; Hodge et al. 1973).

The albacore is a commercially important migratory species of tuna which normally inhabits the epipelagic subtropical and transitional waters of the Pacific, Atlantic, and Indian oceans. In the North Pacific, albacore may undertake transpacific migrations between Japan and the west coast of America (Clemens 1961; Otsu and Uchida 1963; Clemens and Craig 1965).

While single-pass nuclear reactors were operated at Hanford, Wash., the Columbia River was an important source of artificial radionuclides in the Pacific Ocean off Oregon and Washington. Some radionuclides, formed by neutron activation of impurities in river water used to cool the reactors, were transported via the Columbia out into the ocean and were detectable in the plume water far at sea (Osterberg et al. 1965). Cobalt-60 was among the radionuclides carried by the Columbia River effluent (Gross and Nelson 1966). Fallout from nuclear detonations, however, was another source of ^{60}Co (Lowman and Ting 1973; Hodge et al. 1973). Which of these sources was more significant in contaminating tuna is not known. We shall attempt to use the temporal and geographical variations in ^{60}Co content of albacore livers to estimate the relative importance of the two sources and to provide information on migrations of albacore.

Methods

During the period June–October of 1963 through 1969, over 200 albacore livers were removed from fish (520–850 mm fork length, $\bar{x}$ = 640 mm) collected on surface jigs and preserved aboard ships either by freezing or with Formalin.[1] In the laboratory, livers were weighed, dried, ashed (500° to 570°C), ground, and packed into 15-cm^3 plastic counting tubes for radioanalysis. Samples were counted for 100 min using a 12.7-cm^2 NaI (Tl) crystal detector with a 512 channel pulse-height analyzer. See Pearcy and Osterberg (1968) for additional details on collection and analysis. Results are expressed in picocuries per gram wet weight to be compatible with other published results on cobalt in tuna livers.

Results and Discussion

Concentrations of ^{60}Co in the livers of albacore caught in three general regions along the west coast of North America are shown in Figure 1 for 1964. Of all the years, 1963–69, this year provided the most data for inter-regional and temporal comparisons. Two general trends are evident:

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

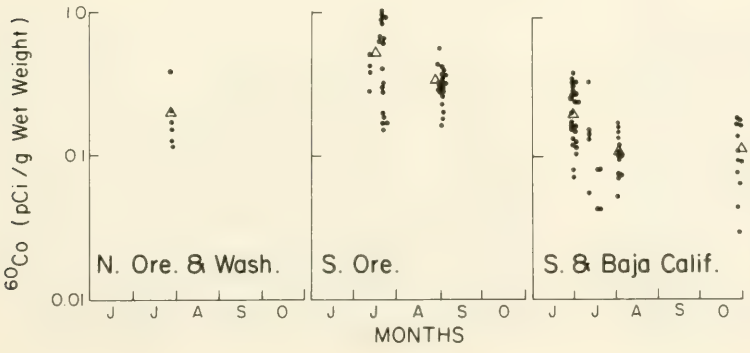

FIGURE 1.—Cobalt-60 concentrations (dots = actual observations, open triangles = $\bar{x}$ values) from livers of albacore captured off three west coast regions during June-October 1964.

first, relatively high ^{60}Co activities were seen off the southern Oregon coast and somewhat lower concentrations off northern Oregon and Washington as well as off southern and Baja California; second, ^{60}Co concentrations decreased with time during the summer–fall period. Data from other years corroborated these trends.

Annual variations of ^{60}Co in albacore off the Oregon coast (dots and solid line in Figure 2) indicate that ^{60}Co concentrations increased from 1963 to 1964 then declined steadily until 1967, but increased again in 1968.

There are two possible sources of ^{60}Co for albacore in the northeastern Pacific. Until 1965, eight Hanford reactors were a relatively constant source of ^{60}Co entering the Columbia River (Gross and Nelson 1966). In 1965, however, a sequence of shutdowns of individual reactors began (Foster 1972). The other possible source of this isotope is fallout from atmospheric tests of nuclear weapons which also varied in time, but according to a different pattern (Lowman and Ting 1973; Hodge et al. 1973). Inputs of ^{60}Co into the environment by atmospheric tests that could directly effect the activity levels in the North Pacific include over 100 U.S. and U.S.S.R. tests in 1961–62 and Lop Nor, China, tests in 1964–65 (one test each year), 1966 (three tests), 1967 (two tests), and 1968 (one test) (U.S. Environmental Protection Agency 1960–72).

The relatively constant input from the Hanford plant fails to account for the low ^{60}Co values observed in albacore during 1963 nor the increased values in 1964 (Figure 2). Other evidence indicating that Hanford was not the major ^{60}Co source is based on our knowledge of the migration of albacore into the Pacific Northwest fishery and their subsequent movements. Albacore often first appear off the southern Oregon coast and move northward and inshore as the summer progresses (Powell et al. 1952; Keene 1974), sometimes along the axis of the warm Columbia River plume waters (Pearcy 1973). Levels of ^{60}Co did not increase with residence time of albacore in Oregon waters or proximity to the Columbia River in northern Oregon (Figure 1), as would be expected if Hanford was the main ^{60}Co source.

These trends are opposite of those noted in albacore livers for ^{65}Zn, a radionuclide that was known to be associated with the Columbia River effluent, but are similar to those of ^{54}Mn, a radionuclide associated with atmospheric fallout (Pearcy and Osterberg 1968). We conclude, therefore, that most of the ^{60}Co we find in albacore livers was

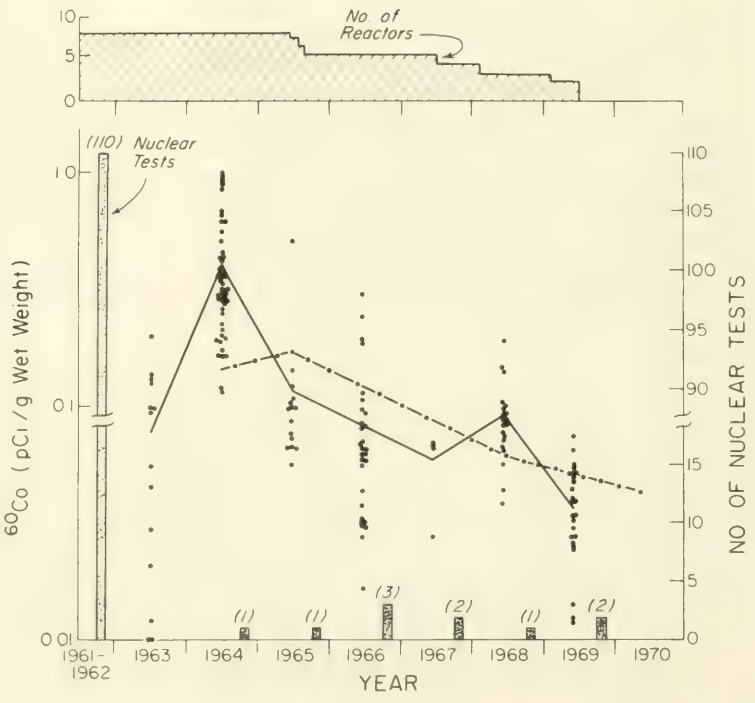

FIGURE 2.—Concentration of ^{60}Co in livers of albacore captured off Oregon and Washington. Solid line indicates mean values of our observations (dots); broken line is a plot of ^{60}Co levels off southern and Baja California as presented by Hodge et al. (1973). Also indicated is the number of Hanford reactors in operation and the number of nuclear atmospheric tests (bars = pre-1963 non-Chinese testing affecting the North Pacific and post-1963 testing at Lop Nor, China) which occurred during our study period.

derived from fallout, even off the coast of Oregon where the influence of the Columbia River plume should be the greatest.

Since radioactivity originating from fallout is higher in the open ocean than in coastal waters where upwelling occurs (Pillai et al. 1964; Folsom and Young 1965; Gross et al. 1965), the spatial-temporal trends evident in Figure 1 may be explained by the residence time of albacore in coastal waters. Highest levels of ^{60}Co are expected in oceanic waters off southern Oregon in June and July; lower levels are expected later in the season after albacore have migrated northward and shoreward and have resided in coastal waters, provided that the biological half-life of ^{60}Co in tuna livers is short enough. The decrease in ^{60}Co levels in albacore (Figure 1) is much more rapid than would be expected from natural radioactive decay of 5.26 yr. Biological turnover must be rapid in order to produce a short effective half-life.

Hodge et al. (1973) related the levels of ^{60}Co in albacore to fallout deposition and found that maximum uptake of ^{60}Co by albacore lagged nuclear atmospheric detonations by 1–2 yr. Annual changes of ^{60}Co concentrations observed off Oregon (Figure 2) show a similar delayed response, but the peak activity levels in albacore occurred a year earlier than the peaks seen by Hodge et al. (1973) off southern California (dashed line, Figure 2). The main atmospheric input by nuclear detonations occurred in 1961–62. Our main peak of ^{60}Co in albacore occurred in 1964, and that reported by Hodge et al. occurred in 1965, indicating a delay of about 2 and 3 yr respectively after testing before the uptake is observed in albacore. This not only suggests that the source of ^{60}Co in albacore is from atmospheric fallout, but that the availability of the radionuclide was different between the albacore caught off California and those caught off Oregon, perhaps because of differences in distributions and migratory patterns than those described by Clemens (1961).

Laurs and Lynn (1977) presented data that confirm this suggestion. Based on recapture of tagged albacore and length-frequency distributions, they concluded that the albacore population found off Oregon is different from that found off southern and Baja California. They further suggest that albacore which migrate into Oregon waters may come from a portion of the offshore population which is located north of the 35th parallel, while those that move into the California waters are located south of the 35th parallel.

The bomb detonations at Lop Nor (lat. 40°N) gave the heaviest fallout input into the North Pacific at about this latitude. Due to the circulation in the North Pacific (Sverdrup et al. 1942), it appears quite possible that albacore which were associated with waters north of lat. 35°N may have experienced high levels of ^{60}Co up to a year before the tuna associated with waters to the south. Circulation in the North Pacific and the latitudinal differences in the location of the two portions of the albacore population appear to be a plausible explanation for the difference of 1 yr in activity peaks between albacore caught off Oregon by us and those off southern and Baja California by Hodge et al. (1973).

Acknowledgments

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LENGTH–WIDTH–WEIGHT RELATIONSHIPS FOR MATURE MALE SNOW CRAB, *CHIONOCOETES BAIRDI*

Snow crabs have been exploited commercially in Alaska since 1961 (Alaska Department of Fish and Game 1975). *Chionocoetes bairdi* is the predominant species with *C. opilio* composing up to 25% of the catch from the Bering Sea. Landings were small and intermittent in the early 1960's but increased to about 3.2 million lb in 1968. Landings expanded dramatically thereafter and exceeded 60 million lb in 1974, with an ex-vessel value of more than $12 million.

Carapace width measurements have been collected from the commercial snow crab catch by biologists since the inception of the fishery; individual weights, however, are not routinely collected because the task is rather time-consuming. The relationships between carapace width, length, and body weight are of interest to biologists and processors. The relationship between carapace length and width is of interest because the carapace shape is one of the diagnostic characteristics to distinguish between *C. bairdi* and *C. opilio* and hybrids of the two species (Karinen and Hoopes 1971). The relationships between carapace width and weight and carapace length and weight have many uses. They are, for example, indicators of condition, used to calculate biomass, and used to estimate recovery of edible meat from crabs of various sizes.

Materials and Methods

Carapace length and width and body weight measurements were taken from 240 mature male *C. bairdi* from commercial catches made south of the Alaska Peninsula in the vicinity of the Shumagin Islands in May 1975. Length and width measurements were taken to the nearest millimeter with vernier calipers and weights were recorded to the nearest gram. Length was measured from the posterior medial edge of the carapace to the anterior medial point of the right orbit. The rostrum was not included in the length measurement because it often erodes when crabs are carried in the live tank of fishing vessels. Width was measured at the widest part of the carapace and included the lateral branchial spine. Width ranged from 128 to 185 mm, weights from 635 to 2,230 g, and lengths from 92 to 143 mm.

The basic linear regression formula $W = a + bL$ was used to express the relationship between width (W) and length (L). Weight (Wt) was related to width and length by the power functions, $\log_{10} Wt = \log_{10} a + b \log_{10} W$ and $\log_{10} Wt = \log_{10} a + b \log_{10} L$. The constants a and b were determined empirically.

Results

The length–width, length–weight, and width–weight relationships are summarized in Table 1. All relationships were characterized by very high correlation coefficients. No relationships between length, width, and weight have previously been reported for *C. bairdi*.

TABLE 1.—Length–width, length–weight, and width–weight relationships for mature male *Chionocoetes bairdi*. [Sample size was 240 animals for each relationship.]

Relationship	Coefficient	Formula
Length–width	0.96	$W = -3.584 + 1.268L$
Length–weight	0.99	$\log_{10} Wt = -3.076 + 2.956 \log_{10} L$
Width–weight	0.99	$\log_{10} Wt = 3.363 + 2.936 \log_{10} W$

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TEMPORAL ASPECTS OF CALLING BEHAVIOR IN THE OYSTER TOADFISH, *OPSANUS TAU*

The oyster toadfish, *Opsanus tau* (Linnaeus), produces two calls: an agonistic grunt and a boatwhistle associated with courtship (Fish 1954; Tavolga 1958, 1960; Gray and Winn 1961). The boatwhistle is produced only by males on nests (Gray and Winn 1961) and is endogenously driven as well as influenced by calling of surrounding males (Winn 1964, 1967, 1972; Fish 1972). A toadfish, not hearing other males, may still boatwhistle for long periods and attract a female. Although toadfish may be influenced to call by the calling of adjacent males, one would assume the circadian patterning of the boatwhistle to be influenced by photoperiod and the fish's behavioral strategy relative to it. Additionally, the rate of calling may be a key to a male's internal state. Calling rate has been manipulated experimentally (Winn 1967, 1972; Fish 1972; Fish and Offutt 1972), but no one has studied the calling rate of undisturbed individual fish. This note is a preliminary attempt to look at these twin problems (when and how fast toadfish call) by recording the boatwhistles of individual males on their nests.

Materials and Methods

Terra cotta drainage tiles were set out individually adjacent to the pilings of a dock at Solomons, Md. Male toadfish which settled into three of the tiles started calling, and the calls were monitored between 9 and 15 June 1969. Because of changing tapes and mechanical problems, the record was not continuous. The recording system consisted of individual Clevite[1] oyster (CH 15-J) hydrophones with their own General Electric Phono-Mic preamplifiers (UPX-003C) and a Precision Instrument Model 207 multichannel tape recorder. The gain was turned down so that only boatwhistles from the fish in the tile adjacent to the hydrophone would present a loud signal. The tapes were transduced onto strip chart paper (Bruel and Kjaer level recorder type 2305), and segments equivalent to 6 min of real time were continuously marked on the chart paper. The number of boatwhistles in each segment was counted.

Results

The activity patterns for the three fish appear aperiodic (Figure 1; Table 1). All of the animals called both day and night (11 calling periods day, 9 night), and the total number of boatwhistles produced for day and night was similar (7,905 day, 6,202 night). Considering the data on a calls-per-hour basis, since daylight hours exceed nighttime in June, does not appreciably alter the results. The fish averaged 41.3 boatwhistles/h during the day and 46.1/h at night from recordings covering 191.5 h of daylight and 134.5 h of darkness. Not only were crepuscular peaks absent, but dawn and dusk appeared irrelevant as cues for calling behavior. There are similarities between certain periods in the data, such as the nights of 14 and 15 June for channel 2, but these similarities are a

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

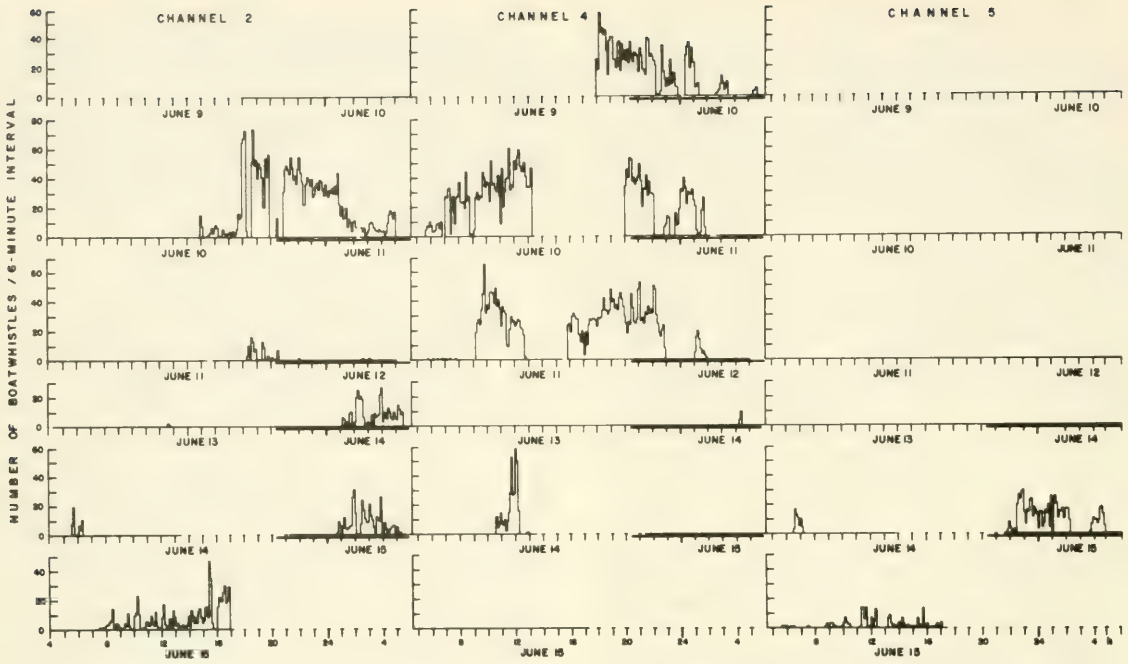

FIGURE 1.—Temporal record of boatwhistle production for each of three toadfish. A missing baseline indicates gaps in the record, and the horizontal line below the baseline indicates the period of darkness.

TABLE 1.—Number of boatwhistles produced during 24-h periods by three toadfish.
[L is light, D is dark, and dash indicates no data.]

Date	Channel 2		Channel 4		Channel 5	
	L	D	L	D	L	D
June 9-10	0	0	849	951	0	0
10-11	890	1,838	2,315	1,103	0	0
11-12	87	11	2,435	848	0	0
13-14	4	364	0	14	0	0
14-15	51	354	355	0	63	719
15	650	—	0	—	206	—
Total	1,682	2,567	5,954	2,916	269	719
Periods called	5	4	4	4	2	1
Total D/total L	1.53		0.49		2.67	

minor feature of the record. Each of the fish produced different numbers of boatwhistles and exhibited separate patterns of calling (Figures 1, 2; Table 1) that were not obviously correlated with each other. One fish (channel 4) boatwhistled twice as much during the day as at night, while the other two (channel 2 and 5, respectively) called 1.5 and 2.7 times more at night than during the day. These ratios from Table 1 change to 2.24, 0.66, and 3.92, respectively when considered on a per-hour basis.

In order to see how fast individual fish called, we constructed histograms of the frequency of occurrence of number of boatwhistles in the 6-min segments (Figure 2). Even though the distributions for day and night were statistically different (Kolmogorov-Smirnoff test), they were combined in each of these histograms. Since these day-night differences have already been mentioned and were inconsistent between fish (Table 1), it seemed reasonable to present differences between the fish rather than differences between day and night.

Data from the three channels were combined to show the calling rate from all boatwhistles recorded in this study (Figure 3). It is obvious that toadfish remain quiet for long periods (Figure 1). For Figures 2 and 3, all quiet periods of 60 min or longer were arbitrarily excluded. Still, zeros accounted for close to 20% of all intervals measured (Figure 3). From the cumulative percent curve (Figure 3), it is striking how strongly the distribution is skewed toward the low end. Over 50% of the intervals measured had $\leq$ 1 to 2 boatwhistles/min (ca. 10 calls/6 min), and over 75% of the intervals had $\leq$4 to 5 boatwhistles/min. Only 10% of the intervals contained calls emitted at a rate of 6 or more per minute. Finally less than 1% of the intervals contained calls emitted at a rate of 10 to 12/min. Although an animal may have called for

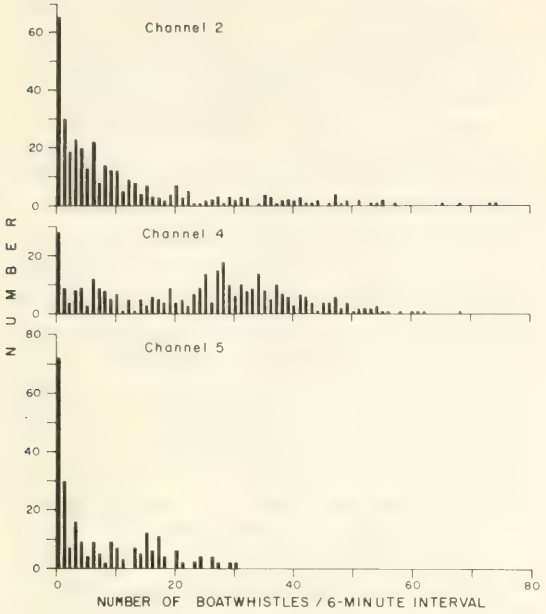

FIGURE 2.—Histogram of frequency of occurrence (i.e., "number" on Y-axis) of number of boatwhistles in 6-min intervals (X-axis) for each of three toadfish. Silent periods of an hour or longer were excluded from the analysis.

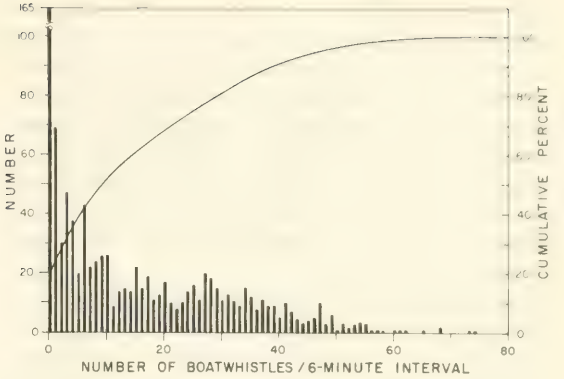

FIGURE 3.—Histogram of frequency of occurrence (left axis) and cumulative frequency of occurrence (right axis) of number of boatwhistles in 6-min intervals combined for the three toadfish. Silent periods of an hour or longer were excluded from the analysis.

many hours (Figure 1), the number of calls fluctuated markedly. High rates of calling were often strongly peaked, i.e., not maintained for long periods.

Discussion

The only obvious feature of the data from this study (Figure 1; Table 1) is its lack of patterning or predictability. Clearly, the recordings indicate no diel cycle. While they do not rule out the possibility of maximal or minimal periods of sound production for a toadfish population (Breder 1968), it appears unlikely that individuals would be synchronized to any great degree. It is difficult to reconcile these results with the periodicity of the in-air respiration data of Schwartz and Robinson (1963) and the impressions of Tavolga (1960) and Schwartz and Robinson (1963) that the toadfish is basically nocturnal. Squirrelfishes are active at night, when they are least vocal (Winn et al. 1964; Salmon 1967; Bright 1972; Bright and Sartori 1972), and likewise toadfish might not have a clear vocalization rhythm, while maintaining rhythms for respiration or other functions.

The rate of calling by fish in this study was low, and individuals lapsed into silence for long periods. This result verifies our experience from playback studies (Winn 1967, 1972; Fish 1972; Fish and Offutt 1972); fish were often silent, forcing us to sample many tiles to find a male calling rapidly enough for use in an experiment. For this reason preplayback calling rates, equivalent to control calling rates, were biased upward. From 68 experiments, each with sample sizes ranging between 11 and 16, Winn's (1972) preplayback data (recalculated) show a mean of 22.41 ± 4.3 (1 SD) boatwhistles/3 min, or an average of 7.5 calls/min. In his initial playback experiments, Winn (1967) increased the calling rate to an average of 11.46, 11.70, and 11.48 boatwhistles/min by playbacks of 18, 26, and 36 boatwhistles/min. Playbacks of 10 calls/min did not increase calling. Fish (1972) found that with optimally spaced playbacks, he could increase their rate to 14 to 16 sounds/min (1 call every 3.7 to 4.3 s). He called this pace the maximum sustained calling rate. Fish's data combined with Winn's indicate that when competing with other males, the toadfish does not grade his output uniformly, but follows more of a step function, i.e., his calling is either facilitated or not. In one chance encounter Fish (1972) observed a male calling 25 times/min as a female approached his shelter.

Our fish called considerably below their capabilities. However, calling rates of 11 and 12/min would suggest that the males were sexually receptive. It will take more work to establish what is normal for the toadfish and what abiotic

and biological factors control motivation during the season. An unspawned male and a once-spawned male guarding eggs, might call at different rates. Schwartz (1974) and Lowe (1975) have indicated spawning peaks, which could be related to calling motivation. Although calling decreases, boatwhistles are still emitted after the assumed mating season (Fine 1976) It is not possible to accurately place the period of 9–15 June 1969 in a spawning peak or lull.

Density within a toadfish population will also affect sound production since calling fish facilitate each other. There could also be a tonic facilitation (Schleidt 1973), so that fish hearing boatwhistles, even if below the stimulatory rate, would be more prone to call than would a solitary male. It is also possible that some populations of toadfish could be limited by shelter availability for male nesting. At the dock at Solomons, where these recordings were made, shelter was provided primarily by our tiles placed along the dock pilings. Since the area was largely clear of rocks, tin cans, and boards which might provide shelter, the density of calling fish in the experimental area was not high, and we might not expect a great deal of facilitation.

Acknowledgments

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BIOLOGY AND HOST–PARASITE RELATIONSHIPS OF *CYMOTHOA EXCISA* (ISOPODA, CYMOTHOIDAE) WITH THREE SPECIES OF SNAPPERS (LUTJANIDAE) ON THE CARIBBEAN COAST OF PANAMA

Although parasitic isopods of the family Cymothoidae have been described from both freshwater and marine fishes, relatively little is known of their biology and host–parasite relationships (Morton 1974). Probably all species of cymothoids are protandrous hermaphrodites, with the male larvae settling out of the plankton onto the mouth, body surface, body cavity, or gills of their host. After a period of maturation, males of some species become associated with the buccal cavity where they undergo a sex change. Both broad and limited host specificities have been described for members of the Cymothoidae (Trilles 1964).

Here we comment on the biology and occurrence of *Cymothoa excisa* Perty on three sympatric species of Caribbean snappers: *Lutjanus synagris* (Linnaeus), *L. analis* (Cuvier), and *Ocyurus chrysurus* (Bloch). Host–parasite relationships and infestation rates are discussed and evidence is provided suggesting that this parasite does little, if any, damage.

Methods and Materials

All specimens were collected along the Caribbean coast of the Republic of Panama and the Canal Zone, near the Smithsonian Tropical Research Institute's Galeta Marine Laboratory. Samples were taken in sea grass habitats consisting primarily of *Thalassia testudinum,* using a 4.9-m otter trawl with 1.3-cm bar mesh. Details of the trawling program and site descriptions are given in Heck (in press). All material was sorted in the laboratory and subsequently preserved in 10% Formalin.[1]

Fishes from which parasites had been removed were wet weighed after blotting. Standard lengths of fishes were measured to the nearest 0.5 mm, and total lengths and widths of isopods were measured to the nearest 0.01 mm, using dial calipers. Individual isopods were sexed according to the presence of an appendix masculina on the second pleopod (males) or from the development of oostegites and presence of larvae (females). The Montalenti femininity index [F.I. = $W/L \times 100$, where W = width and L = length (Montalenti 1941)] was used for the isopods as a measure of the degree of transformation from male to female.

Fulton's coefficient of condition [$K = W/L^3$, where W = wet weight and L = standard length (Ricker 1971)] was used to assess the well-being of fish in relation to the presence or absence of isopods. Values of K were computed for 30 infested and 30 isopod-free individuals in each of the three species of snappers, *L. synagris, L. analis,* and *O. chrysurus.* An arc–sin transformation was performed on K values before statistical analyses were carried out.

Results and Discussion

Cymothoa excisa was found to occur on 4.7% (32/681) of the *L. synagris,* 10.5% (16/152) of the *L. analis,* and 2.1% (11/527) of the *O. chrysurus* collected. Adults of the two snapper genera exhibit different habitat preferences: members of the genus *Lutjanus* prefer near-bottom habitats with ample cover, while *O. chrysurus* inhabits the open-water column above coral reefs. Juveniles of all three species are commonly associated with sea grass beds, and it may be during this stage of their life cycle that infestation occurs. This is suggested by the occurrence of metamorphosed parasites in very small fish (20–30 mm SL). In addition, a linear relationship exists between lengths of the isopod and those of its host (Figure 1), which further suggests that fishes are infested early in life with subsequent growth by both host and parasite. Six male parasites differed significantly from this relationship, however, and each of these occurred jointly (or in triplicate) with a much larger female. Previously, Bowman (1960) reported that pairs of isopods (*Lironeca puhi* Bowman) were nearly always present in the gill cavity of the moray eel *Gymnothorax eurotus* (Abbott). In our specimens, pairs (or triplicates) were found in only 6.8% of the parasitized fishes and during sorting no free isopods were found which might have escaped from the mouth cavity. Unless male isopods were differentially lost during the trawling operations, it appears that the population biology of cymothoid genera can be quite different.

Several other species of lutjanids collected showed no indication of isopod infestation. For example, none of the 53 *Lutjanus griseus* (Linnaeus) nor any of the 19 *L. apodus* (Walbaum) contained *C. excisa.* Differences in habitat prefer-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

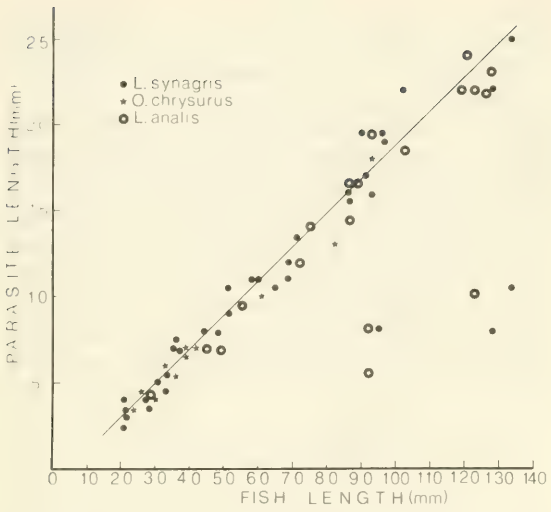

FIGURE 1.—Relationship between *Cymothoa excisa* and lutjanid lengths. Least squares line was fit excluding the six points which fall far below the cluster of other points. These six points represent males which occurred jointly with females.

ences may be responsible for the absence of cymothoids on these species. It is also possible that nonparasitized snapper species are cleaned of parasites by cleaner fishes and decapod crustaceans on nearby reefs.

All isopods were attached to the tongue and oriented anteriorly with smaller males positioned behind females. Some degeneration and possibly some scar tissue were evident at the base of the tongue, but not elsewhere in the mouth. The mouth parts of *C. excisa* seem adapted for piercing and sucking and Morton (1974) has postulated that cymothoids are hemophages. As expected, females of *C. excisa* are proportionately wider than males, and the transition from male to female appears to occur in the 13- to 19-mm size range (Figure 2).

Bowman (1960) presented evidence that the presence of a female suppresses feminity in cooccurring males, as expressed by the Montalenti index. We found just the opposite result: males occurring jointly with females displayed a significantly higher average femininity index than males which occurred alone (Figure 2); (t-test, $P<0.01$). The reason for this difference is unknown.

Because *C. excisa* filled so much of the mouth cavity of infested snappers, it seemed, a priori, that the presence of isopod parasites must interfere with feeding. However, several crustacean families, including Xanthidae (*Micropanope* sp., *Pilumnus* sp., *Panopeus* sp.), Porcellanidae (*Petrolisthes* sp.), Squillidae (*Squilla* sp.), Penaeidae (*Penaeus* sp.), and Alpheidae (*Alpheus* sp.), were represented in the gut contents of the infested snappers. Moreover, there were no significant differences between coefficients of condition calculated for parasitized and unparasitized fish in any of the three lutjanids (t-test, $P = 0.01$). Thus it appears that any harmful effects due to the presence of parasites are not reflected in either the ability to capture prey or in overall health, as measured by K. It is possible, however, that the presence of isopod parasites may lower fitness by causing increased mortality during periods of stress (Keys 1928), by reducing the reproductive output of infested fish, or by decreasing the ability of parasitized individuals to avoid predators. Although the requisite data are lacking to test the first two premises, we were able to test the latter possibility indirectly using the following reasoning: If predation is not selective for parasitized individuals, then a similar distribution would be expected for each group. This was tested by assigning both parasitized and nonparasitized individuals of all three species to 20-mm (SL) size classes for all but the largest fish (excluded because of small sample size). There was no significant difference between the two groups ($\chi^2 = 6.69$, $P = 0.05$).

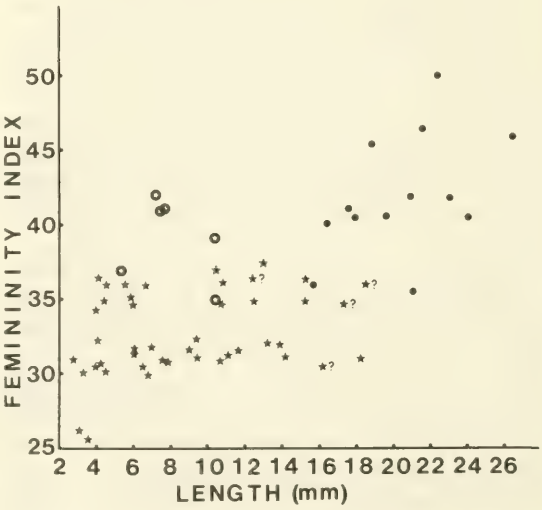

FIGURE 2.—Femininity index in *Cymothoa excisa*. Legend: * = male, • = female, o = male occurring jointly with female, *? = sex indeterminate.

On the basis of these results and the data previously presented, we consider *C. excisa* to be a relatively benign parasite. This appears to be a general characteristic of host–parasite relationships between cymothoids and fishes, at least in unstressed situations (Keys 1928).

Acknowledgments

Specimens of *C. excisa* were kindly identified by T. Bowman, U.S. National Museum of Natural History (USNM), and have been deposited at the USNM. C. M. Courtney, Marco Ecology Laboratory, Marco Island, Fla., sexed the parasites and analyzed gut contents of parasitized fishes. D. T. Logan and M. H. Baslow provided comments on the manuscript.

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FECUNDITY OF THE SOUTHERN NEW ENGLAND STOCK OF YELLOWTAIL FLOUNDER, *LIMANDA FERRUGINEA*

The yellowtail flounder, *Limanda ferrunginea*, is an important commercial species to both the New England and Canadian fishing industries. According to Royce et al. (1959) there are five relatively distinct stocks of yellowtail flounder with little migration occurring between them: southern New England, Georges Bank, Cape Cod, Nova Scotian, and Grand Bank stocks. Catches have recently been declining. For example in the southern New England and Cape Cod stocks (ICNAF (International Commission for the Northwest Atlantic Fisheries) subarea 5Zw), the number of metric tons landed per standard fishing day has declined from 3.5 in 1970 to 1.5 in 1975; the total catch declining from 24,103 to 5,460 metric tons over the same period (Cain[1]).

Pitt (1971) has estimated the fecundity of the Grand Bank stock (ICNAF Subareas 3L, 3N, 3O) but no other yellowtail flounder fecundity data have been published. Fecundity may vary from one stock of flatfish to another, e.g., plaice (Simpson 1951), so we have analyzed the fecundity of the southern New England stock of yellowtail based on 50 fish, and compared these values with the fecundity estimates of Pitt (1971).

Methods and Materials

Ovaries used for fecundity estimates were collected on 9 and 12 April 1976 from fish landed by commercial vessels at Point Judith, R.I. Fish were randomly sampled from the combined catches of several vessels, and therefore represented a random sample of the southern New England population. Only ripening ovaries, i.e., ovaries swollen but eggs not fully developed in size (Scott 1954), were used thus omitting fish that may have begun to spawn. Fish were measured to the nearest centimeter total length, and the ovary wet weight was determined to the nearest 0.1 g. Ovaries were preserved in Gilson's fluid as modified by Simpson (1951) and allowed to remain in this solution for 3-5 mo to facilitate ovarian tissue breakdown. Otoliths, read independently by each of us, were used to determine ages. The growth rings were recognized according to Scott (1954) who also

[1]Cain, W. L. 1976. Yellowtail flounder tabulations for 1977 assessments. Int. Comm. Northwest Atl. Fish. Working Pap. No. 76/IV/49.

demonstrated the validity of the use of otoliths for the age determination of yellowtail flounder.

Eggs were separated from the ovarian tissue by washing with a gentle stream of water through a series of four fine mesh screens (mesh sizes 1.52, 0.98, 0.51, 0.14 mm). After separation the eggs were placed in a gallon jar and diluted with water to 3,000 ml. Large samples were first divided using a plankton splitter and only half of the sample diluted. The lid of the gallon jar was modified to hold a 1-ml Hensen-Stemple pipette which extended approximately 15 cm into the jar. The jar was then inverted 10 times and the sample taken before any settling of the eggs occurred. The subsample was placed onto a gridded Petri dish and the eggs counted with a dissecting microscope. A minimum of three subsamples were counted for each fish. The coefficient of variation was computed and ranged from <1 to 18% (mean = 7.5%). Fecundity was estimated by multiplying the mean number of eggs from the subsamples by 3,000, or 6,000 if the sample had been split.

Results and Discussion

Linear regressions, correlation coefficients (r), and coefficients of determination (r^2) were computed from data transformed to common logarithms. These were:

$$F = 0.986L^{3.858} \quad \text{(Figure 1)} \quad (1)$$
$$r = 0.885,\ r^2 = 0.784$$

$$F = 240{,}700A^{1.294} \quad \text{(Figure 2)} \quad (2)$$
$$r = 0.812,\ r^2 = 0.659$$

$$F = 62{,}150G^{0.678} \quad \text{(Figure 3)} \quad (3)$$
$$r = 0.941,\ r^2 = 0.885$$

were F, L, A, and G are fecundity (10^6 eggs/female), length (centimeters), age (years), and gonad weight (grams), respectively. In all equations the slopes were significantly different from zero ($P < 0.001$).

The coefficient of determination for Equation (3) shows that 88.5% of the variation in fecundity was related to gonad weight independent of both length and age. This was more than the variation related to length alone (78.4%, Equation (1)) or age alone (65.9%, Equation (2)). Furthermore, the correlation coefficient for fecundity vs. gonad weight was significantly higher than that for fecundity vs. length ($t = 3.85$, df = 47, $P < 0.001$), and fecundity vs. age ($t = 4.84$, df = 47, $P < 0.001$). Gonad weight, therefore, contributed most to the variation in fecundity and would be the best parameter to measure in estimating fecundity. However, since the relationship between ovary weight and fecundity varies seasonally, depending on the stage of development, this conclusion may be valid only for prespawning fish.

In addition to the 50 pairs of ovaries collected by us, we estimated the fecundity of 14 fish (lengths 29-46 cm, ages 2-6 yr) from the southern New England stock collected in 1976 by the Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, Mass. The regression lines for fecundity vs. length and fecundity vs. age for these fish were not significantly different ($P > 0.25$) from our regressions when compared

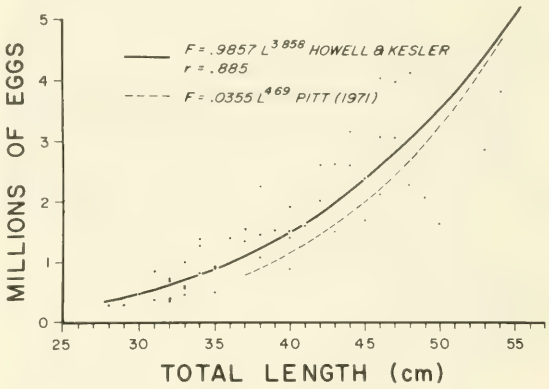

FIGURE 1.—Yellowtail fecundity plotted against length. Solid line is the fitted curve for the southern New England population, and the dashed line that of the Grand Bank population.

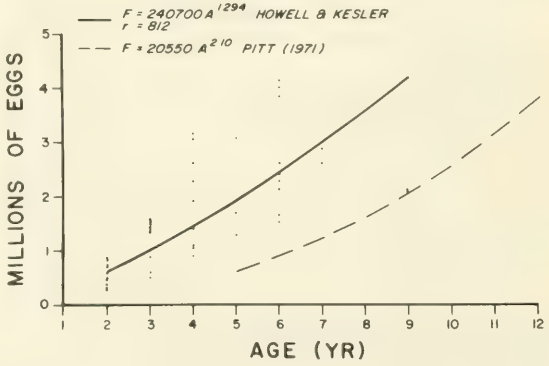

FIGURE 2.—Yellowtail fecundity plotted against age. Solid line is the fitted curve for the southern New England population, and the dashed line that of the Grand Bank population.

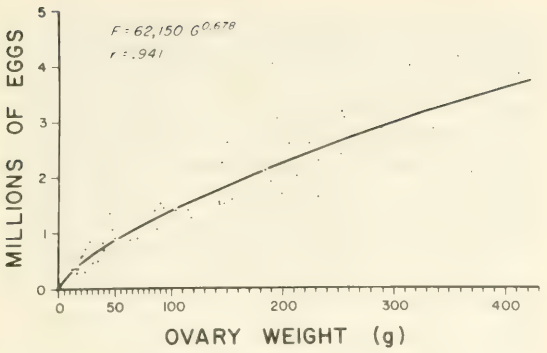

FIGURE 3.—Yellowtail fecundity plotted against ovary weight, and the fitted curve for southern New England.

using an analysis of covariance (Snedecor and Cochran 1967).

We compared our data with those of Pitt (1971) for the Grand Bank stock (lengths 37-54 cm, ages 5-12 yr) using analysis of covariance. The slopes of fecundity vs. length and fecundity vs. age regression lines were not significantly different ($P > 0.25$) (Figures 1, 2). This indicates that the rate with which fecundity increased with both length and age was not significantly different between the two populations. However, the intercepts of the fecundity vs. length regressions were significantly different ($F = 8.67$; df = 1, 94; $P < 0.01$), southern New England fish being more fecund for a given length than Grand Bank fish (Figure 1). In addition, the intercepts of the fecundity vs. age regressions were significantly different ($F = 28.87$; df = 1,92; $P << 0.005$) indicating that southern New England fish were more fecund for a given age (Figure 2).

There may be several reasons why fecundity is higher at a given length and age in the southern New England stock. Several authors including Hodder (1965), Bagenal (1969), and Tyler and Dunn (1976) have suggested that both nutrition and temperature can affect egg production. Little is known about the type and amount of food available to the two populations so no speculation can be made about the possible nutritional effects on fecundity in this species. Water temperatures inhabited by the two stocks are different. Southern New England yellowtail flounder inhabit waters of 4.9–12.3°C (Royce et al. 1959), while Grand Bank yellowtail flounder are found at temperatures of −1° to 6.5°C (Pitt 1974). Pitt (1974) found that the southern New England population grew faster than the Grand Bank population, probably due to these warmer temperatures. This accelerated growth rate apparently results in earlier maturation of the southern New England fish, 50% of the females being mature at 2–3 yr old and 32 cm long (Royce et al. 1959) as compared with 5–6 yr and 37 cm long for Grand Bank females (Pitt 1970). Simpson (1951) found that faster growing plaice were more fecund for a given age and length. Likewise, Pitt (1964) found that in American plaice of comparable ages, ovaries of faster growing fish were larger than those of slower growing individuals, and fecundity was higher. If the ovaries of the faster growing southern New England yellowtail flounder are larger at comparable ages and lengths than those of Grand Bank fish, we would expect southern New England fish to be more fecund, as was the case. The ecological implications of this higher fecundity are unknown and require further study.

Acknowledgments

We thank Robert Livingstone and Judith Penttila of the Northeast Fisheries Center, NMFS, NOAA, Woods Hole, who generously provided us with ovaries and ages of some yellowtail flounder. Thanks go to T. K. Pitt who provided us with the raw data necessary to compare the two stocks, and to S. B. Saila and W. H. Krueger of the University of Rhode Island who critically read the manuscript.

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"MOCK FISH" METHOD FOR STUDYING MICROBIAL INHIBITING AGENTS

In experiments intended to study the effects of various agents or conditions on the microbial outgrowth in food products, it is desirable to approach efficacy similar to those conditions of actual handling and marketing. However, in experiments on fishery products, when one wishes to find effects of an agent or condition, the use of whole fish or fish fillets adds variables to any experimental design. These undesired variables are: variations in the total microbial population and in the composition of the microbial flora from fish to fish; different time intervals and other storage variations in the handling history of fish even from the same catch; different fillet or sample thicknesses which will affect the counts per gram ratio from sample to sample; different physiological conditions, age, wounds, etc., of the fish which might affect experimental comparisons; and possible presence of inherent antibiotics in the substrate. The latter variable does not permit a separation of the antibiotic effects of the additives from the antibiotic effects of the substrate.

In order to study what effects agents might actually have on specific microbial outgrowth in an efficacious situation, a "mock fish," composed of gelatin (containing nutrients) and supported structurally with cheesecloth was devised. The mock fish allowed us to control: total number and composition of the microbial flora; location of microbial contamination, e.g., surface or evenly dispersed throughout the sample; uniformity of distribution of microbes from sample to sample; size and thickness of the samples; and the handling history and physiological state of the samples. This system permits the quantitative recovery of the inoculated microbes by simply melting the gelatin at 31°–32° C.

This note describes the application of mock fish in studying the effects of disodium ethylenediamine tetraacetate (EDTA, Fisher Scientific Co.[1]) with or without an iodophor (Wyandotte Co.) contained in ice for controlling microbial outgrowth of a mixture of four *Pseudomonas* species. This procedure is not recommended as a means of predicting the effectiveness of an inhibitor on a specific species of fish. Its role is to screen inhibiting agents for general effectiveness and to permit a comparison among them.

Materials and Methods

Mixture of *Pseudomonas* Species

Four *Pseudomonas* species, previously isolated from iced fish in our laboratory, were used in these experiments. Each species of *Pseudomonas* was grown in separate Eugon Broth (BBL) test tube culture for 18 h at 20°C. Then 2 ml from each culture were pooled and well mixed in a sterile test tube to prepare an inoculum mixture. From this mixture 1 ml was inoculated into 1 liter of melted gelatin medium described below to give an estimated 10^4 to 10^5 bacteria/ml of the final preparation.

Mock Fish Preparation

1) Cheesecloth discs were cut to size to fit inside glass Petri dishes, and then they were cut in half. The Petri dishes were then sterilized at 121°C for 15 min.

2) Ten milliliters of melted, inoculated 10% gelatin and 1% Eugon Broth medium were pipetted into each sterile Petri dish. A sterile needle was used to make sure that the cheesecloth disc halves did not overlap during gelatin solidifica-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

tion. Once solidified, the gelatin in each plate was cut in half with a sterile needle along the cheesecloth division, thus making two mock fish for use in experimental procedures. The mock fish were gently pried loose from the Petri dish with the aid of a sterile spatula or large, blunt forceps and placed into a beaker containing crushed ice. The cheesecloth provides ample structural support to the solidified gelatin.

Preparation of Crushed Ice

To minimize contamination, distilled water, glassware, ice cube trays, and an ice cube crusher were sterilized prior to use in the preparation of solutions and crushed ice. Using distilled water to minimize the presence of chlorine, minerals, etc., the following solutions were prepared: 1) 1% EDTA; 2) 0.1% EDTA; 3) 1% EDTA plus 1% $CaCl^2$; 4) 0.1% EDTA plus 1% CaCl; and 5) 0.1% EDTA plus 10 ppm of Accord (an iodophore manufactured by BASF Wyandotte Corp., Wyandotte, Mich.).

In order to demonstrate the applicability of this mock fish method, we tested the effect of EDTA embedded in ice on typical *Pseudomonas* species found associated with iced fish. Interest in EDTA for use as a microbial inhibitor has been cited by Levin (1967), Winarino et al. (1971), and Maunder et al.[2] The addition of calcium ions was to interfere with the chelating property of EDTA. The addition of an iodophor was to observe for a possible greater effect.

The control ice contained no added ingredients. These solutions were poured into ice cube trays and frozen. A hand operated individual ice cube crusher was used to prepare crushed ice to fill 800-ml beakers. From 8 to 10 mock fish were placed into each beaker containing crushed ice and stored at 0°C for the duration of the experiment.

Bacterial Assays

At each time interval (0, 1, 3, 6, and 11 days), mock fish were removed from each beaker and placed in a sterile plastic petri dish. The Petri dishes were floated on a 31°–32°C water bath to melt the gelatin. Aliquots of the melted, well-stirred gelatin were decimally diluted and plated using Eugon Agar (BBL) with 0.1% yeast extract (BBL) added. Plates were incubated at 20°C for 5 days prior to counting.

[2]Maunder, D. T., W. P. Segner, C. F. Schmidt, and J. K. Boltz. 1966. Growth characteristics of Type E *Clostridium botulinum* in the temperature range of 34 to 50°F. Annu. Rep. to U.S. At. Energy Comm. (now ERDA), Contract No. AT(11-1)1183.

Results and Discussion

The results of the experiments are shown in Figure 1. The initial starting population was 4.5×10^4 pseudomonads/ml of gelatin medium. The resulting growth patterns reflect the effect of agents contained in the ice and melt water. By the 5th day, melt water entirely surrounded the mock fish in each beaker. By about the 10th day, the floating ice composed one-half to one-third of the beaker contents.

The mock fish held together throughout the experiment with only occasional slivers, not supported by the cheesecloth, breaking off.

The mock fish method permits an evaluation of the effects of microbial inhibiting additives, used singly or in combination, to yield relatively accurate results. Thus, the method may be used to screen a wide variety of antibiotic systems before going into efficacy studies. The value of the mock fish system is that it not only permits a broad screening of additives, but it also permits one to determine, in efficacy studies, whether microbial inhibition is due to additives alone or partly to substrate antibiotic components such as certain polypeptides (J. T. R. Nickerson pers. commun.). It affords a method of controlling some variables and/or allowing the study of effects upon specific microorganisms. We have employed versions of

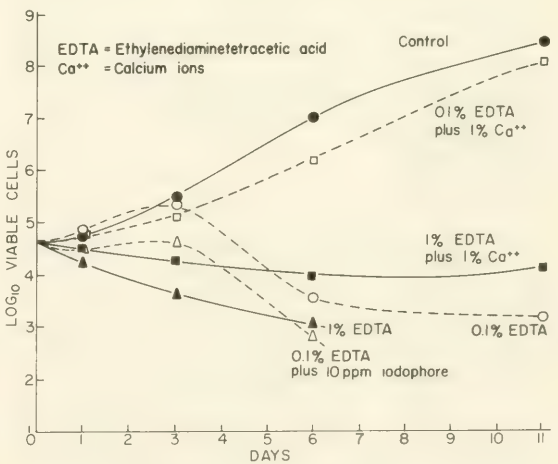

FIGURE 1.—Survival of *Pseudomonas* spp. in mock fish.

mock fish before in irradiation studies in which we either embedded the inoculum evenly throughout the gelatin disc or smeared the same size inoculum on one surface of the gelatin disc (Green and Kaylor 1977). The method might be extended to other applications where some detail or specific effects are to be elucidated.

From Figure 1 it is obvious that 1% calcium ions negate the effect of 0.1% EDTA and reduce the effect of 1% EDTA. An improved effect is noticed when 10 ppm iodophor is coupled with 0.1% EDTA, and this was somewhat expected.

The implied conclusion is that 1% EDTA embedded in ice, free of divalent ions, will reduce the outgrowth of *Pseudomonas* spoilage organisms on iced fish and that the inhibitory effect of 0.1% EDTA combined with 10 ppm iodophor is even greater. The expected results obtained with the mock fish supports their reliability for the intended use, but it is not suggested for use as a substitute for efficacy tests. Therefore, conculsions regarding the effectiveness of inhibitory additives for any specific substrate must ultimately be derived from conventional efficacy tests.

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REPRODUCTIVE CYCLE OF THE PINK SURFPERCH, *ZALEMBIUS ROSACEUS* (EMBIOTOCIDAE)

Embiotocids received early attention from biologists (e.g., Eigenmann 1892) partly because of the viviparous mode of reproduction displayed by fishes of this family. The pink surfperch, *Zalembius rosaceus* (Jordan and Gilbert), is one of the lesser known members of this group. What is most distinctive about *Z. rosaceus* as compared with other embiotocids is the timing of the various events of its annual reproductive cycle. The purpose of this report is to describe this cycle.

Materials and Methods

Specimens were collected off the coast of southern California at depths ranging from 27 to 33 m. Samples were taken from Redondo Beach, Los Angeles County, to San Clemente, Orange County, Calif. Monthly collections were obtained from May 1972 to September 1973 and January and March 1977. Collections were made using otter trawls from the Occidental College RV *Vantuna* and from the RV *Fury II*, operated by the Orange County Board of Education. Specimens from July, August, and September 1973 were provided by the Southern California Coastal Water Research Project. Specimens were also examined in the ichthyology collection of the Los Angeles County Museum of Natural History.

The fish were preserved in 10% Formalin.[1] Gonads were embedded in paraffin. Histological sections were cut at 8 μm and stained with iron hematoxylin followed by eosin counterstain. Gonads were sectioned from the following numbers of females: January (7), February (4), March (11), April (6), May (5), June (10), July (1), August (15), September (18); October (3); December (6); and from 85 males, as shown in Table 1. Sectioned material was collected in 1973 except that for May, June, October, and December 1972.

Results and Discussion

The gonadal morphology and histology of *Z. rosaceus* closely resembles that of the embiotocids *Cymatogaster aggregata* as described by Eigen-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

mann (1892), Turner (1938), and Wiebe (1968) and *Embiotoca jacksoni* by Lagios (1965).

The seasonal testicular cycle is summarized in Table 1. From August to November, testes are regressed with the seminiferous tubules containing mainly spermatogonia and Sertoli cells. Testicular recrudescence (i.e., renewal of the germinal epithelium to start a new cycle) was evident in December. The testicular cycle was far advanced in one December male whose testes contained small clusters of sperm. The major period of spermiogenesis (sperm formation) occurred from March through June (Table 1). Germinal epithelium was exhausted or greatly reduced in seminiferous tubules of regressing testes which were first observed (Table 1) in June males. In these testes, lumina are typically filled with compact sperm cysts called spermatophores by Wiebe (1968). Some breeding may conceivably continue as late as July because residual sperm cysts lingered into this month in the regressing testes of three males. While the exact duration of the mating season is not known for *Z. rosaceus*, the testicular cycle seems to indicate that it encompasses March–June.

Embryos were observed for the first time in ovarian histological sections from 7 of 15 August females. The gestation period appears to last about 5–7 mo as one December and one January female gave birth while in the otter trawl aboard ship, and females that had recently given birth, as well as several that were still gravid, were found in the January and March 1977 samples. The 23 gravid females that were examined contained a mean of 3.5 young (range 2–6). A sample of 26 near-term young that were removed from females during this period averaged 34 mm SL.

There appear to be two trends in the timing of the reproductive cycles of California embiotocids. In the first, breeding occurs mainly during autumn with the young being born in spring and summer. This group includes *Amphistichus argenteus* (Carlisle et al. 1960), *Brachyistius frenatus* (Feder et al. 1974), *Damalichthys vacca* (Feder et al. 1974), *E. jacksoni* (Lagios 1965), *Hyperprosopon argenteum* Rechnitzer and Limbaugh 1952), and *H. ellipticum* (Feder et al. 1974). Young of *D. vacca* may appear as late as October (Feder et al. 1974). In the second group, breeding takes place during the summer with parturition occurring the following spring and summer. This group includes *Amphigonopterus* (= *Micrometrus*) *aurora, Micrometrus minimus* (Hubbs 1921), and *C. aggregata* (Bane and Robinson 1970; Shaw et al. 1974).

The timing of the reproductive cycle of *Z. rosaceus* with mating in the spring and parturition in the winter is a pattern clearly distinct from that currently known for any other California embiotocid. The advantages of this type of cycle are not clear at this time and further studies on the biology of this species will be necessary.

TABLE 1.—Monthly samples of *Zalembius rosaceus* showing percentage of males in various stages of the testicular cycle.

Month	*N*	Spermiogenesis	Partial regression	Total regression	Recrudescence
Jan.	5	0	0	60	40
Feb.	8	50	0	12	38
Mar.	12	75	0	8	17
Apr.	10	100	0	0	0
May	13	100	0	0	0
June	4	75	25	0	0
July	3	0	100	0	0
Aug.	6	0	0	100	0
Sept.	7	0	0	100	0
Oct.	10	0	0	100	0
Dec.	7	14	0	14	72

Acknowledgments

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GALLBLADDER LESIONS IN CULTURED PACIFIC SALMON

This note records observations on a previously unreported biliary lesion in the gallbladders of various samples of coho, *Oncorhynchus kisutch;* chinook, *O. tshawytscha;* and sockeye, *O. nerka,* salmon cultured mainly in Puget Sound, Wash., during 1974–76. There were no obvious signs of distress or physical debilitation in affected fish. The gallbladders were enlarged and impacted with an amorphous yellow or white material which, in some instances, extended into the common bile duct (Figure 1).

Efforts to prove infectious origin were unsuccessful. No bacteria were consistently isolated from gallbladder or hepatic tissues and attempts to demonstrate a viral agent on a chinook cell line were negative. Possibilities of protozoan or helminth parasitism were discounted after microscopic examination of tissues, gallbladder, and intestinal contents.

Normal and impacted gallbladder, liver, and kidney tissues were fixed in 10% buffered Formalin[1] and stained sections were prepared at Northwest and Alaska Fisheries Center (NWAFC), NMFS, NOAA, Seattle, Wash. Excessive vacuolation of the columnar epithelium was evident in affected gallbladders (Figure 2). No lesions were observed in either the livers or kidneys of fish with the gallbladder condition.

Preliminary studies (Table 1) indicate a predominance of an as yet uncharacterized mucopolysaccharide material in impacted gallbladders. Serum bilirubin, cholesterol, and glucose concentrations of coho salmon with impacted gallbladders were not different from those found in normal fish.

TABLE 1.—Composition of material in impacted gallbladders in coho salmon.

Material	Percentage
Solids (dry wt @ 105°C)	30.4
Ash	14.2
Nitrogen	1.25
Reducing sugar (ortho-toluidine method)	11.52

Case History

Impacted gallbladders were first observed in May 1974, when 25 yearling coho salmon from saltwater pens in southern Puget Sound were referred to the disease laboratory at NWAFC Aquaculture Experiment Station near Manchester, Wash., for diagnosis of an unrelated skin infection (Table 2). The condition was detected in four separate lots of coho and chinook salmon in central Puget Sound during the summer growing season of 1974. In July 1975, the lesion was seen in a subsample of 250 chinook salmon smolts in a private freshwater rearing pond in Oregon (Table 2). Several lots of salmon being held for husbandry and disease research at the Aquaculture Experiment Station have also been found to have this condition.

Four thousand 0-age coho salmon smolts (18–20 g) reared on commercially prepared Oregon Moist Pellets (OMP) were transferred to saltwater pens at the Aquaculture Experiment Station in early August 1976 where they continued to receive the same ration. Smolts of the same stock (1,000) were

[1]Reference to trade names does not imply endorsement of the National Marine Fisheries Service, NOAA.

FIGURE 1.—Impacted material can be clearly seen in the gallbladder of affected coho salmon (upper fish). Normal gallbladder (lower fish) is shown for comparison.

TABLE 2.—Occurrence of impacted gallbaldders in Pacific salmon subsampled from saltwater and freshwater rearing areas.

Date	Species	Age	Feed	No. of fish in lot	No. of fish examined	Percentage of fish examined with gallbladder anomalies	Environment and site
May 1974	Coho	1+	OMP[1]	—	25	100	Net pens: South Puget Sound
Oct. 1974	Coho	1+	OMP	100,000	100	90	Net pen: Central Puget Sound
Oct. 1974	Coho	1+	OMP	100,000	100	76	Net pen: Central Puget Sound
Oct. 1974	Coho	1+	OMP	100,000	165	90	Net pen: Central Puget Sound
Oct. 1974	Chinook	0+	OMP	100,000	157	89	Net pen: Central Puget Sound
July 1975	Chinook	0+	OMP	50,000	250	90	Freshwater holding pond: lower Columbia River
Aug. 1975	Sockeye	1+	OMP	450	39	85	Net pen: Research fish, Manchester, Wash.
Sept. 1975	Coho	1+	OMP	250	160	93	Net pen: Research fish, Manchester
Nov. 1975	Coho	1+	OMP	164	164	85	Net pen: Research fish, Manchester
Nov. 1975	Coho	1+	Dry[2]	9,000	600	0	Net pen: Central Puget Sound
Dec. 1975	Chinook	2+	OMP	40	40	0	Cultured brood stock: Manchester
Dec. 1975	Coho	2+	OMP	94	94	0	Cultured brook stock: Manchester
Dec. 1975	Coho	3	Natural	25	25	0	Mature fish returning from sea: Manchester
Dec. 1975	Coho	1+	OMP	500	200	0	Freshwater station: Seattle, Wash.
Jan. 1976	Coho	1+	SC[3]	400	40	0	Freshwater station: Seattle
Jan. 1976	Coho	1+	OMP	66,000	60	99	Net pen: Research fish, Manchester
Oct. 1976	Coho	1+	OMP	1,600	120	75	Net pen: Research fish, Manchester
Oct. 1976	Coho	0+	OMP	1,000	100	0	Freshwater station: Seattle
Oct. 1976	Coho	0+	OMP	4,000	180	38	Net pen: Research fish, Manchester
Aug.–Oct. 1976	Coho	1+	Dry	100,000+	114	37	Net pen[4]: Central Puget Sound

[1]Oregon Moist Pellet — Commercial product.
[2]Commercial dry pelleted ration.
[3]Fish fed experimental OMP diet containing single cell protein.
[4]Pers. commun., D. Weaver, Domsea Farms, Gorst, Wash.

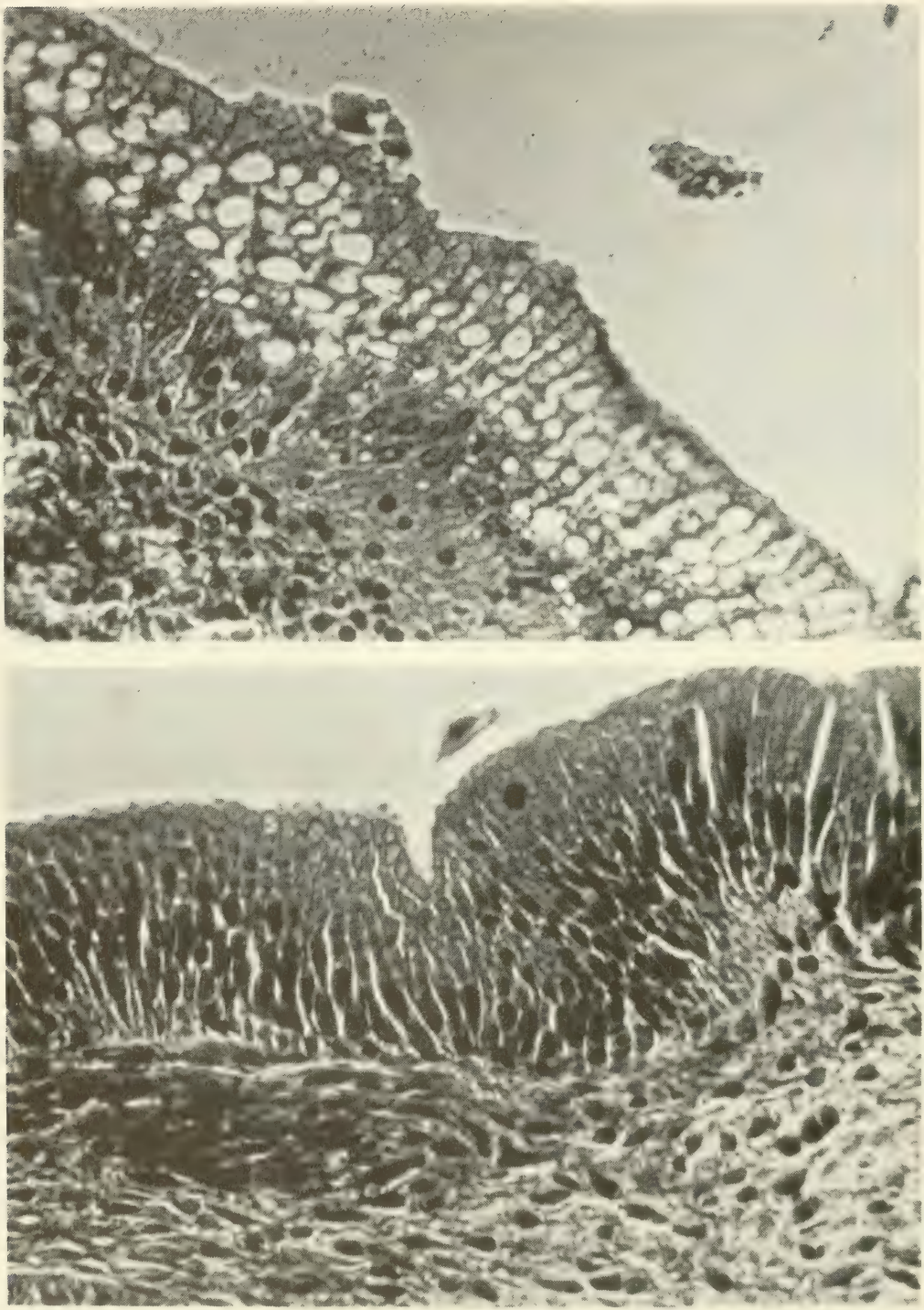

FIGURE 2.—Upper photo shows histopathologic features (vacuolation) of the epithelium from an impacted gallbladder of a small coho salmon cultured in saltwater. Lower photo shows normal epithelium of the gallbladder from a small wild coho salmon collected in saltwater. Hematoxylin-eosin stain; ×320.

held back for freshwater rearing. Approximately 38% of the fish in saltwater were found to have the gallbladder condition by mid-October. The condition did not develop in those remaining in freshwater.

In all cases observed thus far, affected fish were young (<2 yr) salmon that had been reared exclusively on commercially prepared pellets. With the exception of the occurrence in Oregon, all cases of the abnormality have occurred in saltwater net pens.

With dietary adjustments the condition is apparently reversible. In an unrelated nutrition study, 75% of the subsamples of one lot of 1,800 coho salmon that had been fed a ration of OMP for several months had impacted gallbladders. These test fish were divided into two lots. One group (1,400) was fed a laboratory prepared moist pellet diet and the remaining fish (400) were continued on the commercial OMP diet. After 4 mo, subsamples indicated that incidence of abnormal gallbladders in fish on the laboratory diet had been reduced to 5%. Incidence of the condition in the test group maintained on the OMP diet remained at 75%.

Discussion

I have found no published information relative to gallbladder abnormalities in fishes. The pathological features described for this condition do not resemble any infectious disease currently described for fishes and are more suggestive of a toxic or nutritional disorder.

The biliary system is an integral part of the digestive apparatus, playing an important role in lipid digestion. It also provides a mechanism for recycling certain metabolic byproducts of hepatic origin through the digestive system. Many of these metabolic byproducts are excretory wastes while others can be salvaged for reuse by redigestion. Studies as yet do not prove a major detrimental effect of this condition on the fish. Knowing the importance of the biliary system, however, it is inconceivable that it does not have an adverse effect on the animals' nutritional status, particularly in relation to systems dependent upon adequate and diverse lipid supply.

Acknowledgments

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TIMING OF THE SURFACE-TO-BENTHIC MIGRATION IN JUVENILE ROCKFISH, *SEBASTES DIPLOPROA*, OFF SOUTHERN CALIFORNIA

Species of the genus *Sebastes* lead a pelagic existence as larvae, transforming to pelagic prejuveniles and finally benthic juvenile stages at varying sizes (Moser 1967, 1972). Pelagic prejuveniles of some species often congregate under drifting objects (Hitz 1961); off the coast of southern California, *Sebastes diploproa* (Gilbert 1890) is the dominant rockfish species found under drifting kelp (Mitchell and Hunter 1970). Adults of this species inhabit a bathymetric range of 91–578 m and a latitudinal range from Alaska to Baja California (Hart 1973). Little is known about the movement of this rockfish from surface to benthic waters. This paper provides information on the disappearance from surface waters and the appearance in the benthic habitat based on seasonal size distribution from the two habitats.

Materials and Methods

Surface prejuveniles were collected by dip net off San Diego, Calif. (lat. 32°52′N, long. 117°30′W), from beneath drifting kelp (primarily *Macrocystis pyrifera*) during 1975 and 1976. Benthic juveniles were sampled in standard 10-min bottom trawls with a 7.6-m (25-ft) otter trawl (12.7-mm stretch mesh cod end liner) in 1972 through 1976. Most trawls were made in and around the Los Angeles Bight from Point Dume (lat. 34°00′N, long. 118°48′W) to Dana Point (lat. 33°28′N, long. 117°43′W) at depths from 92 to 183 m, although small *S. diploproa* were captured as shallow as 46 m. This does not encompass the entire adult bathymetric range, but younger stages of *Sebastes* generally tend to occupy shallower parts of the adult range (Kelly and Barker 1961; Moser 1967, 1972; Westrheim 1970). Only

those trawls containing one or more specimens of *S. diploproa* were considered, a total of 96 trawls.

Results

Surface dip net collections consisted of 873 prejuveniles, the largest of which was 58.7 mm standard length (SL). A total of 2,418 benthic juveniles were taken in the trawl collections, with the following size breakdown: <30mm, 2; 30–39 mm, 84; 40–49 mm, 892; and 50–59 mm, 1,440. Few prejuveniles larger than 50 mm SL were captured in surface collections (Figure 1); thus they appear to settle out at a size under 50 mm. At this size prejuveniles are about 1 yr old according to laboratory growth measurements (unpublished data) and the growth curve determined by Phillips (1964); this is well within the range of published values for other members of the genus. Age of settlement has been estimated to be 6 mo for *S. umbrosus* (Chen 1971), 4 or 5 mo for *S. marinus* (Kelly and Barker 1961), and 6-12 mo for *S. alutus* (Westrheim 1973; Carlson and Haight 1976).

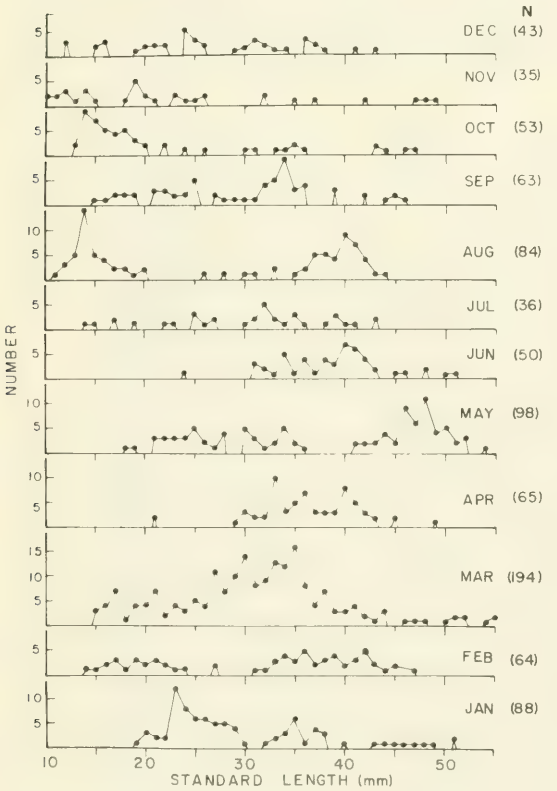

FIGURE 1.—Monthly size distribution for surface prejuvenile *Sebastes diploproa* from the combined dip net collections of 1975–76. Parenthetical numbers indicate numbers of fish collected in that month.

Female *S. diploproa* are ovoviviparous, releasing yolk sac larvae from February to July off California (Phillips 1964). The abundance of newly transformed prejuveniles (10–14 mm SL) in August through December indicates that the principal parturition season occurred in the latter part of this interval (Figure 1). The presence of small individuals in February and March, however, may indicate that there were two principal parturition seasons. Westrheim (1975) provided evidence for two parturition seasons in 1973 off British Columbia (July and October–December) and suggested that this species might release larvae throughout the year.

Surface prejuveniles in the correct size category for settlement were present throughout the year but their abundance was greatest in late spring to early summer. The percentage of specimens larger than 40 mm SL peaked in May and dropped off rapidly thereafter (Figure 2), suggesting that emigration from surface waters occurred primarily in May and June. For comparison, seasonal abundance of pelagic prejuveniles of three other *Sebastes* species are shown (Figure 3). Emigration from surface waters occurred in January to February for *S. rubrivinctus*, May to June for *S. paucispinis*, and July to August for *S. serriceps*.

Benthic juvenile *S. diploproa* occurred in a highly clumped distribution (variance exceeded mean number of fish per trawl for all months with more than one trawl). Since several months were undersampled or lacked a sufficient number of trawls, data were combined by 2-mo intervals (Figure 4). Small benthic juveniles first appeared in July–August; abundance peaked in November–December and tapered off thereafter.

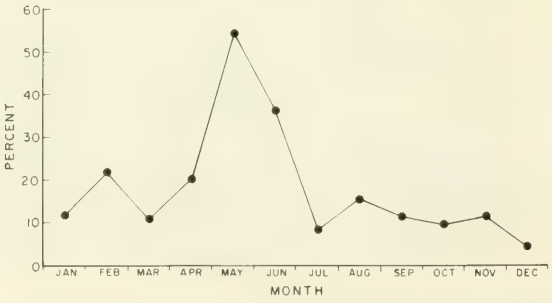

FIGURE 2.—Percentage of surface prejuvenile *Sebastes diploproa* >40 mm SL from the combined dip net collections of 1975–76.

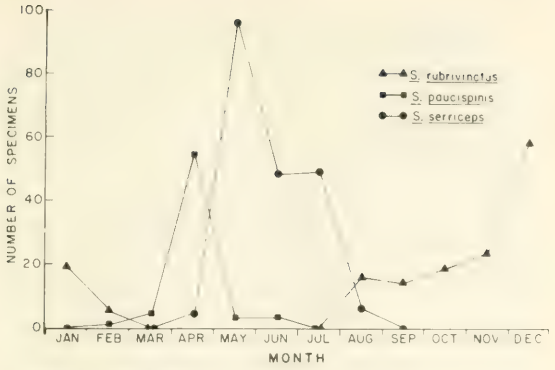

FIGURE 3.—Monthly abundance of surface prejuveniles of *Sebastes rubrivinctus*, *S. paucispinis*, and *S. serriceps* from the combined dip net collections of 1975–76.

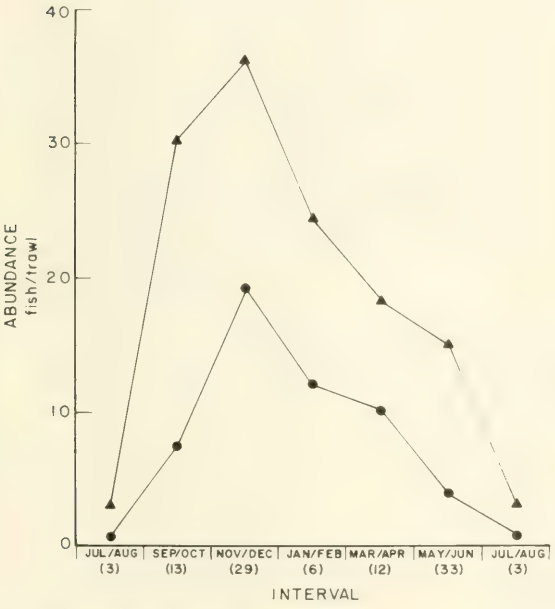

FIGURE 4.—Bimonthly abundance (number caught per trawl) of benthic juvenile *Sebastes diploproa* from trawl collections of 1972 through 1976. Circles represent abundance of all specimens <50 mm; triangles, all <60 mm. Parenthetical numbers indicate the number of trawls made per interval.

Discussion

Surface size distribution and abundance data indicate that the bulk of emigration from the surface occurred in late spring to early summer (Figures 1, 2), whereas appearance of benthic juveniles began in midsummer and continued over a period of several months (Figure 4). The temporal discrepancy between disappearance from the surface and peak benthic appearance suggests that migrant juveniles may occupy an intermediate habitat between emigration and settlement. During this period, the juveniles are probably in midwater, as shown for *S. macdonaldi* by Moser (1972). Four specimens of *S. diploproa* have been taken in two discrete-depth midwater trawls by the RV *Velero IV* and are presently in the fish collection of the Natural History Museum of Los Angeles County (LACM). Three of these specimens (43, 47, 48 mm SL) were captured in October 1970 at a depth of 250 m off San Clemente Island (lat. 32°39′N, long. 118°11′W; LACM 36315-1); the fourth specimen (43 mm SL) was taken in December 1970 at a depth of 200 m off Santa Catalina Island (lat. 33°21′N, long. 118°46′W; LACM 36307-1). Both tows were taken between 0200 and 0430 (local time) over bottom depths of 1,915 and 1,280 m, respectively. Since these bottom depths greatly exceed the bathymetric range for *S. diploproa*, time may be spent in horizontal movement to benthic habitat of suitable depth. Early migrants may come from nearshore areas, such as those sampled in the dip net collections, whereas those appearing later in the year may come from offshore prejuvenile populations; larval *Sebastes* are known to be distributed hundreds of kilometers offshore (Ahlstrom 1961).

Southern California is near the southern end of the geographic range for *S. diploproa* (Phillips 1964); no information was available on the surface prejuveniles of this species from the center or northern parts of its range. Extension of the timing of emigration and subsequent appearance in the benthic habitat is probably a direct result of the long parturition season off California. Westrheim (1975) has shown that two parturition seasons may occur per year off British Columbia and has suggested that limited year-round spawning may take place. In general, however, as one goes further north, the principal parturition season is progressively shorter and later; off Oregon, the season is mid-May to June (Hitz 1962), June to July off Washington (DeLacy et al. 1964), and July off British Columbia (Westrheim 1975). I would expect surface prejuvenile year classes to be more distinct in the north than shown in my data (Figure 1), and that timing of emigration from surface waters would be more precise.

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